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Freezer on, lights off! Environmental effects on activity rhythms of fish in the Arctic

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Circadian rhythm, biotelemetry, photoperiod, behavioural ecology, *Salvelinus alpinus*, seasonal activity

Abstract

Polar regions are characterised by acute seasonal changes in environment, with organisms inhabiting these regions lacking diel photoperiodic information for parts of the year. We present, to our knowledge, the first high-resolution analysis of diel and seasonal activity of free-living fishes in polar waters (74°N), subject to extreme variation in photoperiod, temperature and food availability. Using biotelemetry, we tracked two sympatric ecomorphs of lake-dwelling Arctic charr (*Salvelinus alpinus* n=23) over an annual cycle. Charr activity rhythms reflected the above-surface photoperiod (including under ice), with diel rhythms of activity observed. During the dark winter solstice period, charr activity became arrhythmic and much reduced, even though estimated light levels were within those at which charr can feed. When twilight resumed charr activity ensued as diel vertical migration, which continued throughout spring and increasing day-length, despite stable water temperatures. Diel activity rhythms ceased during polar day, with a sharp increase in arrhythmic fish activity occurring at ice-break. Despite contrasting resource use, circannual rhythms were mirrored in the two ecomorphs, although individual variability in activity rhythms was evident. Our data support conclusions of functionally adaptive periods of arrhythmicity in polar animals, suggesting maintenance of a circannual oscillator for scheduling seasonal behavioural and developmental processes.

Introduction

Fitness depends on forecasting the optimal timing of season-specific activities, such as migration, hibernation and reproduction, to exploit optimal conditions[1]. Organisms are able to anticipate seasonal conditions by use of photoperiod, a predictable environmental signal or cue[1]. In polar regions extreme seasonal changes occur, driven by rapidly shifting day length. This results in periods of several months per year when the sun remains permanently above (polar day) or below (polar night) the horizon, limiting the diel photoperiodic information polar organisms receive, as the amplitude of diel light level change is minimal during these periods. The daily molecular oscillator or circadian clock coordinates many aspects of physiology, metabolism and behaviour [e.g. 2,3], and is usually entrained by the light/dark cycle[3]. This pervasiveness of circadian rhythms suggests that circadian clocks are functionally adaptive[1], yet some high-latitude species present periods of around-the-clock activity[4] suggesting that the expression of an internal circadian clock is temporally uncoupled, or possibly lacking[4, 5]. For example, under constant summer light conditions Svalbard reindeer (*Rangifer tarandus platyrhynchus*) show intensive feeding activity with an absence of circadian rhythmicity. In order to anticipate and prepare for forthcoming seasonal events such species alternatively possess functional, circannual clocks[4, 5].

The Arctic charr (*Salvelinus alpinus*), “charr” hereafter, is the most northerly-distributed freshwater fish. It is adapted for life in cold, dark and nutrient poor environments, and is capable of foraging at low temperatures and light levels (<1°C, <0.001 lux)[6, 7]. Polymorphic populations of lake-dwelling charr commonly occur, and divergence follows ecological gradients that correlate with the number and availability of habitats and food resources[8]. These sympatric discrete phenotypes constitute ecomorphs that differ in morphology and ecological traits. At high-latitudes where charr have access to the sea, anadromous forms also occur, which undertake annual, short-lasting feeding migrations during summer[9]. Thus, these high-latitude aquatic environments are characterised by acute temporal and spatial variations in food availability.

We present the first year-round study of individual fish activity levels, in response to Arctic conditions, through acoustic tracking of co-occurring ecomorphs of lake-dwelling charr. We hypothesised that during periods of distinct light-dark cycles diel rhythms of fish activity would occur, but that during polar night, insufficient distinction between dark and lighter phases would result in loss of rhythmicity and reduced fish activity. We also expected that during polar day, activity levels would remain high and arrhythmic, with circannual activity rhythms alike in both charr ecomorphs.

Methods

a) Study area and data collection

Lake Ellasjøen (maximum depth, 34m), is located on Bear Island (74°30'N, 19°00'E), a high-Arctic island. Temperature loggers (Vemco: V13T-1L) recorded water temperature over the study period (1/9/2009–12/8/2010). The lake showed negligible summer stratification, but an inverse temperature gradient occurred over winter, inferring the likely period of ice coverage (16/12/2009–24/5/2010, 158 days).

Charr were tracked using an underwater, autonomous acoustic telemetry array, the VR2W Positioning System (Vemco, Halifax, Canada). Details of the tracking experiment are explained in Hawley *et al*[10]. Briefly, fish were implanted with tags yielding time-stamped positions of longitude, latitude and depth, allowing individual fish displacement to be calculated from the three-dimensional distance between consecutive positions. Tracking data was obtained for two ecomorphs, a littoral epibenthic (littoral) form (*n*=13) and an offshore zooplanktivorous (pelagic) form (*n*=10).

b) Data analysis

Individual mean values of fish displacement and depth were calculated from tracking data for each hour (0-23) of each calendar week (figure1, figureS1 for 95% C.L.). To determine whether individual displacement or depth use differed between hours, we employed *Linear Mixed Effect*s models with hour as a predictor, for littoral or pelagic ecomorphs and photoperiod categories (see table1 and supplementary methods). To assess heterogeneity in displacement within individuals, Welch's *ANOVA* were applied with hour as a factor predictor for each photoperiod category for each individual (tables S7, S8 and supplementary figures for 95% C.L.). To evaluate the probability of type II error due to limited sample size power simulations were conducted on the Welch's *ANOVAs* (table S5). Analyses were conducted in JMP Pro13 (SAS institute Inc.) and R (version 3.3.3).

Results

For both ecomorphs a significant effect of hour was observed in displacement during the light/dark- decreasing photoperiod (*a*), dark (*b*(i)), light/dark- increasing photoperiod (*c*) and ice-covered polar day (*d*(i)) categories of photoperiod (table1, figureS1). During the period of absent twilight (*b*(ii)) a significant effect was observed for littoral charr only. No significant hour effect was shown for either ecomorph during the weeks of winter solstice (*b*(iii)), or the period of ice-free continuous light (*d*(ii)). No effect of hour was observed on fish depth, except for the period of increasing photoperiod (*c*) where a significant effect was revealed in both littoral and pelagic ecomorphs (table1).

Individual variation in displacement was evident, particularly among littoral-morph fish, with 18 and 42% of littoral charr showing a significant effect of hour during the two polar-day periods respectively (*d*(i)), (*d*(ii)) (tables S7,S8). 10% of pelagic and 46% littoral fish responded to the variable hour of day during the period of absent twilight (*b*(ii)). No individuals from either morph exhibited an hour effect during the winter solstice (*b*(iii)).

Discussion

Our findings show that charr activity rhythms reflect the above-surface photoperiod (including under ice), with diel rhythms of activity observed, except when the diel amplitude of change in solar irradiance was weakest, at the winter solstice and during the polar day. Our data also show evidence for individual variability in the strength of activity rhythms within both ecomorphs. This is, to our knowledge, the first full-year analysis of diel and seasonal activity of free-living fishes in polar waters, and contributes evidence to the high diversity of biological rhythms at polar-latitudes by describing a functional circannual rhythm largely mirrored in conspecifics.

Seasonal activity rhythms of Ellasjøen charr are concordant with previous descriptions of distinct periods of feeding and growth in charr[7], typified by summer satiation and food deprivation in winter, which presumably have developed as a response to the seasonal differences in water temperature and food availability at high-latitudes[7]. Diel rhythms of activity were observed for much of the year in Ellasjøen charr, with greatest activity recorded during dawn, dusk and daylight. Charr are visual feeders and are capable of foraging for food at very low temperatures and light levels[6]. It is likely, therefore, that charr were able to detect changes in sub-surface irradiance, even during polar-night and under ice[11]. The cessation of diel activity rhythms during the darkest period around the winter solstice, and the sharp increase in arrhythmic activity during the ice-free polar day indicates that the amplitude of change in sub-surface irradiance was too weak to be detected by Ellasjøen charr. Sensory information about daily and seasonal photoperiod is required for the entrainment of circadian and circannual rhythms[1]. Thus, similarly to Svalbard reindeer, the output rhythms of an internal circadian clock maybe temporarily uncoupled or unsynchronised in constant light/dark, coinciding with periods of food abundance and scarcity. The re-emergence of diel rhythms, immediately after the winter solstice, when the sun remained 6° or more below the horizon (twilight absent), indicates anticipation of spring, with diel vertical migration continuing throughout spring and increasing day-length, despite stable water temperatures. In charr, the timing of appetite return after winter is thought to be controlled by internally timed changes in appetite regulation[12], and when held at constant low temperature and given food in excess, captive offspring of anadromous charr maintain seasonal rhythms of food intake and growth[13]. The persistence of circannual rhythms, even when environmental cycles are absent must therefore depend upon internal mechanisms which regulate appetite and energy homeostasis on a seasonal basis[9].

Littoral charr were seemingly more sensitive to distinguishing light/dark transitions, maintaining rhythmicity even when twilight was absent. However no differences in photoreceptor cells and visual pigments between charr forms have been found[14]. Individual variability in activity rhythms was evident, consequently the mechanisms controlling circadian rhythms in Ellasjøen charr may be somewhat plastic, a recent concept of speculation[15], with variation in circadian behaviour considered an independent axis of fish personality[16]. Both ecomorphs of Ellasjøen charr present synchronous, distinct seasonal rhythms. Because of the freshwater-sea smoltification transition in juveniles and a narrow sea-sojourn migration window, circannual rhythmicity is likely more defined in anadromous than in land-locked charr forms[9, 11].

We propose that the daily and seasonal activity rhythms observed in Ellasjøen charr indicate the possible presence of a circannual oscillator, when distinct cycles of feeding, growth and reproduction are functional for a fish adapted for life in the freezer.

Ethics

Experimental protocols were conducted according to approved guidelines, and authorised by the Norwegian national authority for animal research (Forsøksdyrutvalget, ref. 2010/136894-1).

Data accessibility

The data underlying this study are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.6k294[17]

Authors' contributions

M.C.L and C.M.R conceived the study, G.N.C, C.M.R and K.L.H collected the data. K.L.H, T.O.H, C.M.R and M.C.L analysed the data and drafted the manuscript, and all authors revised it. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interest

We have no competing interests.

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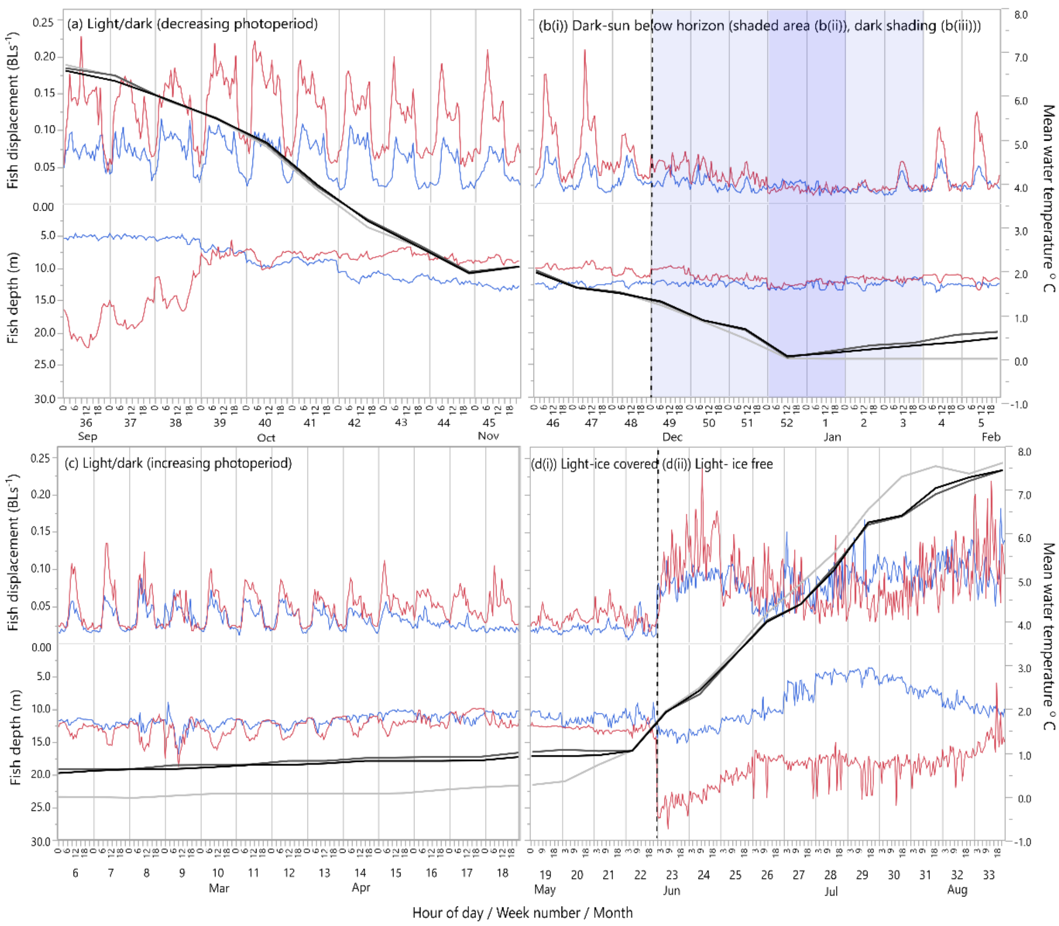
Table1: Test results of *LME* analysis for response variables; fish displacement (BLs^{-1}) and depth (m) with predictor hour (23*df*), for littoral (*n*=13) or pelagic (*n*=10) ecomorphs and photoperiod categories: (*a*) Light/dark-decreasing photoperiod, (*b*(i)) Dark-sun below horizon, (*b*(ii)) Dark- twilight absent, (*b*(iii)) Dark-winter solstice, weeks 52,1, (*c*) Light/dark- increasing photoperiod, (*d*(i)) Light –ice covered and (*d*(ii)) Light- ice free. Data were derived from telemetry of Ellasjøen Arctic charr, weekly individual hourly mean values were used, total *n*=24,053, *n* of individuals varies between photoperiod categories (tableS1). Individual fish identification was modelled as a random effect (table S2, 95% confidence limits were calculated figureS1). A first-order autocorrelation structure (AR1) was modelled as a repeated effect (table S2). Kenward–Roger approximation was used to estimate degrees of freedom (*df*den).

	Littoral morph fish							Pelagic morph fish						
	Fish displacement				Fish depth			Fish displacement				Fish depth		
Photoperiod category	*n*	*df*den	*F*	*p*	*df*den	*F*	*p*	*n*	*df*den	*F*	*p*	*df*den	*F*	*p*
(*a*) Light/dark	3108	907.0	13.4206	<.0001	927.2	0.0599	1.0000	2348	671.0	7.3226	<.0001	695.4	0.3641	0.9975
(*b*(i)) Dark-sun below horizon	3687	1117.3	9.5418	<.0001	1069.2	0.4197	0.9930	2812	756.6	4.2312	<.0001	762.0	0.0566	1.0000
(*b*(ii)) Dark-twilight absent	2127	1935.9	2.1269	0.0014				1615	462.0	1.2829	0.1722			
(*b*(iii)) Dark-winter solstice	580	494.2	0.7441	0.8003				472	369.0	0.4763	0.9815			
(*c*) Light/dark	3915	1041.1	8.3657	<.0001	1037.8	1.5493	0.0476	2735	740.1	12.1192	<.0001	710.9	3.3968	<.0001
(*d*(i)) Light-ice covered	1131	1012.6	2.7669	<.0001	1018.0	0.9077	0.5884	734	640.3	1.6073	0.0364	652.0	1.2711	0.1784
(*d*(ii)) Light-ice free	2611	2381.0	1.4373	0.0815	2431.4	1.1533	0.2780	972	863.5	0.9237	0.5662	878.0	0.8980	0.6019

Figure1: Hourly average values of fish displacement (body lengths per second, BLs^{-1}) and depth calculated per calendar week (*n*=24,053) for tracked littoral (blue *n*=13) and pelagic (red *n*=10) Arctic charr ecomorphs from Lake Ellasjøen. Values are presented for photoperiod categories; (*a*) Light/dark- decreasing photoperiod, (*b*(i)) dark- sun below horizon, (*b*(ii)) Dark-twilight absent, sun more than 6° below horizon (shaded area), (*b*(iii)) Dark-winter solstice (dark-blue shading), (*c*) Light/dark- increasing photoperiod, (*d*(i)) Light-ice covered and (*d*(ii) Light –ice free. Weekly mean water temperature (°C) measured at 3 (light-grey), 25 (dark-grey) and 31 (black) metres is plotted for each calendar week. Dashed lines on the date axis show estimated timing of ice-formation (week 49) and break-up (week 23).



Supplementary material

Kate L. Hawley, Carolyn M. Rosten, Thrond O. Haugen, Guttorm Christensen and Martyn C. Lucas. **Freezer on, lights off! Environmental effects on activity rhythms of fish in the Arctic**. *Biology Letters.*

Supplementary Methods – statistical analysis

The positional data was pre-treated in order to filter lower quality positional fixes due to both suboptimal geometry between receivers, and daily environment-induced noise within the system (for more details see [1]). The frequency of detections derived from 19 stationary 'synchronisation' tags (V13-1L) distributed within the receiver array (for locations see [1]) were used to test for heterogeneity in the diel spatial-temporal variation in the total number of detections derived by the acoustic telemetry system over the study period (photoperiod categories A-D, see below). A non-significant interaction effect of synchronisation tag x hour x photoperiod was observed (*GLM*: $n = 15706$, 1242*df*, $F = 0.70$, $p = 0.99$), indicating noise to be constant in time and space throughout the study period for the synchronisation tags. As the synchronisation tags transmit at higher power (they derive millisecond synchronisation of the receiver-positioning array) than the tags implanted into the sampled charr, a control 'fish' tag was also used to test for heterogeneity in the number of positions derived per hour, in Lake Ellasjøen. We observed no hour x photoperiod effect on the mean number of positions derived by the positioning system per hour, per week ($n = 478$, 89*df*, $F = 0.25$, $p = 0.99$), indicating noise to be constant over time-of-day for the duration of the study, within the area of the lake covered by four receivers detecting signals from the control fish tag (located at 439964.7 E and 8255562.6 N (UTM 34) at 15 metres depth).

Individual mean values of fish displacement and depth were calculated from Arctic charr tracking data for each hour (0-23) of each calendar week. To assess whether charr activity or depth use differed between hours, we employed Linear Mixed Effects models (*LMEs*)[2], with hour as a categorical predictor, for littoral or pelagic charr ecomorphs and each photoperiod category: A) Light/dark, with decreasing photoperiod, B1) Dark (polar night)– sun below the horizon, B2) Dark (polar night)– twilight absent, sun more than 6° below horizon, B3) Dark (polar night)– winter solstice, sun more than 6° below horizon (weeks 52, 1)], C) Light/dark, with increasing photoperiod, D1) Light (polar day)– ice covered and D2) Light (polar day)– ice free[1]. Gross patterns of fish activity were compared as average relative displacement between fixes, given in body lengths per second, BLs^{-1} to standardise for body length. Though this is a measure of speed, we describe it as displacement since activity is in all cases likely to be underestimated (since valid fish detections were on average approximately every 80 minutes). Where a shift in photoperiod category occurred mid-week, values from that entire week were included, so that only complete weeks were analysed for each photoperiod category. Data from week number 53 (2009), were combined with week 52 data. A first-order autocorrelation structure (AR1) was included in the *LME* to account for the autocorrelation of time series data and individual fish identification was modelled as a random intercept effect to account for observational dependency caused by repeated individual measures. Estimates of variance among (random effect) and within (residual) individuals are stated, as well as the estimate of autocorrelation in the model (AR1) (table S2). Hourly 95% confidence limits were calculated on the raw data (n=162,530) and are presented in figure S1. Estimates and standard error of hour effect are also given for fish displacement (tables S3, S4) and depth (tables S5, S6). To assess diel heterogeneity in displacement within individuals, we used Welch's *ANOVA* tests (allowing for variance

[1] The manuscript uses lower case letters and Roman numerals, instead of the capitalised lettering and Arabic numerals adopted throughout this document.

heterogeneity) with hour as a categorical predictor for each photoperiod category for each charr individual (tables S7, S8, supplementary figures). Bonferroni correction was applied (adjusted significance level based on 23 individual tests per photoperiod: $p = 0.002$), and 95% confidence limits were calculated and presented in the supplementary figures. Track durations differed for individuals (table S1 and supplementary figures of individual fish tracks), with a reduced number of individuals towards the end of the study resulting in larger confidence limits, values of *n* for each study week are stated in figure S1. The sample sizes were limited by the increasing probability of tag code collisions with greater numbers of active tags in a restricted area [3] and by the relative availability of the two morphs during the short field campaign. To evaluate the probability of type II error due to limited sample size, power simulations based on parametric resampling (number of resamples = 10,000) were performed for the Welch's *ANOVAs* (power values (π) reported in tables S7, S8). For analyses with $\pi < 0.8$, simulations to estimate Least Significant Number of observations (LSN) were conducted, none of which attained LSN estimates below the maximum observation limit, set as two per hour (given our code-repeat rate of 80 minutes). All statistical analyses were performed in JMPPro (v.10.0 SAS Institute, USA) and R (version 3.3.3) [4].

Supplementary Results

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Table S1: Summary information of telemetry derived data for sampled Arctic charr from Lake Ellasjøen, Bear Island. The total number of data positions and individuals are stated for each category of photoperiod: A) Light/dark, with decreasing photoperiod, B1) Dark (polar night)– sun below the horizon, B2) Dark (polar night)– twilight absent, sun more than 6^{o} below horizon, B3) Dark (polar night)– winter solstice, sun more than 6^{o} below horizon, C) Light/dark, with increasing photoperiod, D1) Light (polar day)– ice covered and D2) Light (polar day)– ice free.

Photoperiod category	Start date (week no.)	End date (week no.)	*n* weeks	*n* positions	*n* individuals	mean *n* positions per individual per week	mean *n* positions per individual per hour per week
A) Light/dark– decreasing photoperiod	01/09/2009 (36)	06/11/2009 (45)	10	41 916	23	1822	1.08
B1) Dark– sun below horizon	07/11/2009 (46)	02/02/2010 (5)	12	26 474	23	1151	0.57
B2) Dark– twilight absent (sun more than 6^{o} below horizon)	29/11/2009 (49)	12/01/2010 (3)	7	14 117	23	614	0.52
B3) Dark– winter solstice (weeks 52 and 1)	20/12/2009 (52)	2/1/2010 (1)	2	6 055	23	263	0.78
C) Light/dark– increasing photoperiod	03/02/2010 (6)	28/04/2010 (18)	13	43 752	22	1989	0.91
D1) Light (polar day)– ice cover	29/04/2010 (19)	24/05/2010 (22)	4	13 060	22	594	0.88
D2) Light (polar day)– ice free	25/05/2010 (23)	12/08/2010 (33)	11	17 156	21	817	0.44

Figure S1: Hourly (0-23) mean values and 95% confidence limits of fish displacement (BLs^{-1}) calculated per calendar week for tracked littoral (blue) and pelagic (red) Arctic charr ecomorphs from Lake Ellasjøen, the number of individuals is stated for each week. Photoperiod category (A-D2) is stated alongside week number (36-33). Mean water temperature ± standard error for each week is also given. Ice formation was predicted to occur week 49, break-up week 23. ToD=time of day.

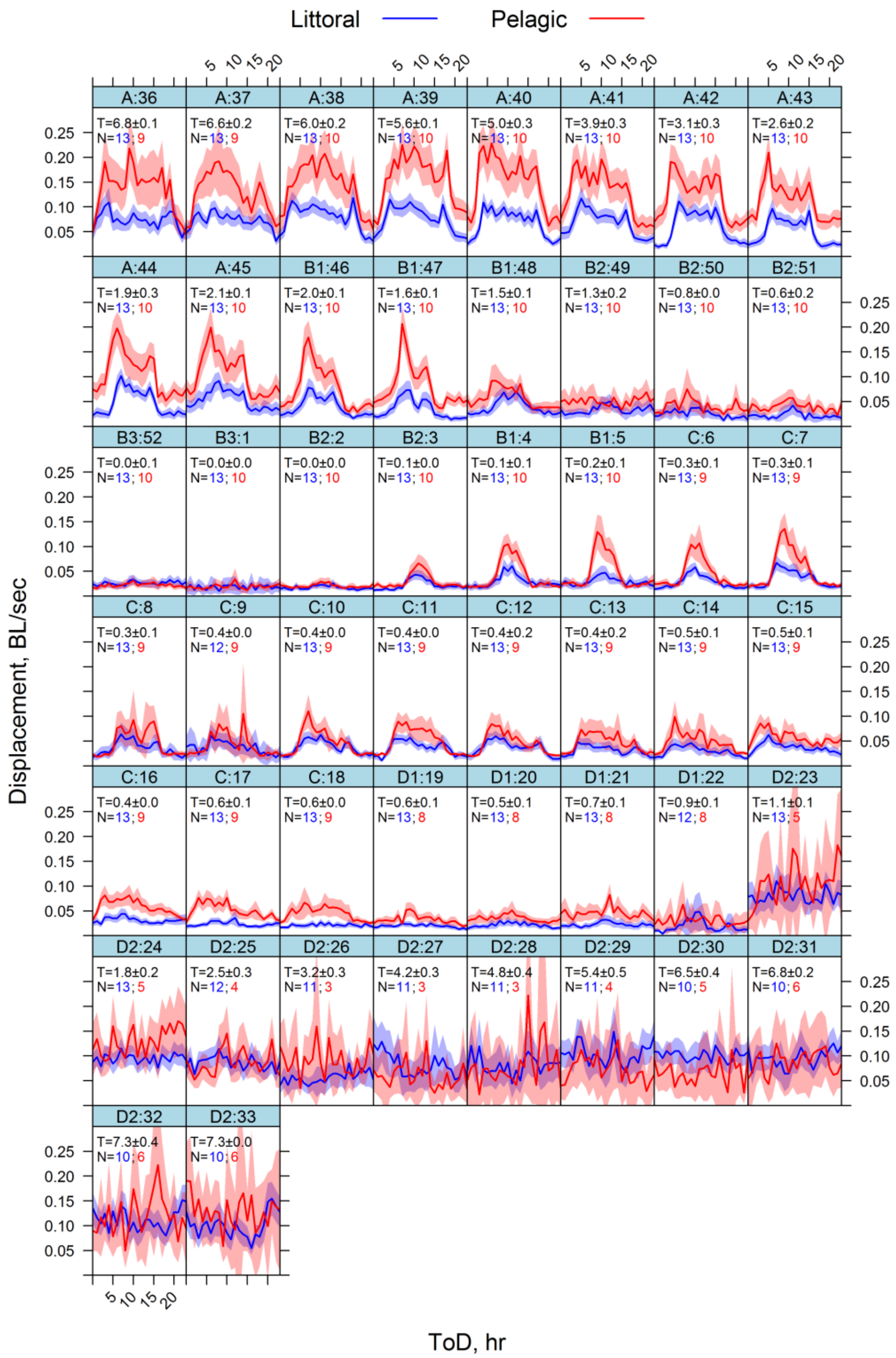


Table S2: LME estimated values of variance among individual (random effect-fish ID) and within (residual) Arctic charr individuals, estimates of covariance in the model (AR1) are also stated. The response variables; fish displacement (body lengths per second) and fish depth (metres) were modelled with predictor hour (23 *df*), for littoral (*n*=13) or pelagic (*n*=10) charr ecomorphs and the photoperiod categories: A) Light/dark, with decreasing photoperiod, B1) Dark– sun below horizon, B2) Dark– twilight absent, sun more than 6 ° below horizon, B3) Dark– winter solstice, sun more than 6 ° below horizon (weeks 52 and 1), C) Light/dark, with increasing photoperiod, D1) Light (polar day)– ice covered and D2) Light (polar day)– ice free. Data were derived from telemetry of Ellasjøen Arctic charr, weekly individual hourly mean values were used, total *n*=24,053, *n* of individuals varies between photoperiod categories (table S1).

	Littoral morph fish						Pelagic morph fish					
	Fish displacement			Fish depth			Fish displacement			Fish depth		
Classification of photoperiod	Fish ID	AR(1)	Residual	Fish ID	AR1(1)	Residual	Fish ID	AR(1)	Residual	Fish ID	AR(1)	Residual
A) Light/dark– decreasing photoperiod	0.0006	0.3545	0.0016	30.2744	0.5209	25.1423	0.0019	0.4505	0.0071	14.7488	0.5194	40.9124
B1) Dark– sun below horizon	0.0006	0.2126	0.0006	80.3432	0.2743	5.4123	0.0004	0.4946	0.0020	15.9704	0.4058	7.7350
B2) Dark– twilight absent	0.0004	0.4652	0.0004				0.0015	0.1213	0.0009			
B3) Dark– winter solstice	0.0009	0.3733	0.0003				0.0000	0.4532	0.0002			
C) Light/dark– increasing photoperiod	0.0003	0.4001	0.0008	73.4598	0.4211	5.3171	0.0004	0.3235	0.0015	17.3048	0.4242	10.6905
D1) Light (polar day)– ice covered	0.0001	0.5709	0.0003	71.5898	0.7909	3.0255	0.0016	0.3031	0.0008	38.3380	0.7947	2.0073
D2) Light (polar day)– ice free	0.0009	0.4376	0.0033	24.7871	0.8954	29.1056	0.0018	0.3362	0.0051	33.3946	0.8852	25.0482

Table S3: Estimated values of hour effect and standard error, generated from a LME for the response variable fish displacement (body lengths per second, BLs^{-1}) for littoral charr ecomorphs (*n*=13). Values are given for each photoperiod category (A-D2), intercept hour[0-23].

	A		B1		B2		B3		C		D1		D2	
	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.
Intercept	0.0338	0.0086	0.0198	0.0066	0.0201	0.0062	0.0223	0.0091	0.0212	0.0058	0.0145	0.0036	0.0886	0.0103
hour[1-0]	0.0082	0.0066	0.0015	0.0033	0.0027	0.0023	0.0010	0.0042	-0.0004	0.0044	0.0017	0.0025	-0.0036	0.0057
hour[2-1]	0.0078	0.0066	0.0011	0.0033	-0.0013	0.0023	-0.0048	0.0041	0.0006	0.0044	-0.0012	0.0025	-0.0071	0.0058
hour[3-2]	0.0152	0.0066	-0.0009	0.0033	-0.0004	0.0023	0.0032	0.0041	0.0060	0.0044	0.0014	0.0025	0.0073	0.0059
hour[4-3]	0.0106	0.0066	0.0033	0.0033	0.0025	0.0023	0.0033	0.0042	0.0079	0.0044	0.0013	0.0024	0.0015	0.0059
hour[5-4]	0.0029	0.0066	0.0002	0.0033	0.0009	0.0023	-0.0036	0.0042	0.0048	0.0044	-0.0015	0.0025	-0.0004	0.0059
hour[6-5]	0.0118	0.0066	0.0026	0.0033	-0.0028	0.0023	0.0038	0.0042	0.0055	0.0044	0.0042	0.0025	0.0009	0.0059
hour[7-6]	0.0002	0.0066	0.0044	0.0033	-0.0001	0.0023	0.0020	0.0042	0.0044	0.0044	0.0020	0.0025	0.0079	0.0059
hour[8-7]	-0.0066	0.0066	0.0044	0.0033	0.0034	0.0023	-0.0060	0.0043	-0.0012	0.0044	0.0023	0.0025	-0.0091	0.0060
hour[9-8]	-0.0042	0.0066	0.0050	0.0033	0.0048	0.0023	0.0076	0.0042	-0.0033	0.0044	0.0013	0.0024	-0.0055	0.0060
hour[10-9]	0.0032	0.0066	-0.0006	0.0033	0.0034	0.0023	-0.0011	0.0041	0.0024	0.0044	0.0062	0.0024	0.0021	0.0060
hour[11-10]	-0.0038	0.0066	0.0004	0.0033	0.0007	0.0023	-0.0015	0.0043	-0.0068	0.0044	0.0026	0.0024	-0.0082	0.0060
hour[12-11]	-0.0051	0.0066	-0.0017	0.0033	-0.0036	0.0023	-0.0025	0.0043	-0.0014	0.0043	-0.0053	0.0024	0.0099	0.0059
hour[13-12]	0.0033	0.0066	-0.0040	0.0033	-0.0057	0.0023	-0.0070	0.0042	-0.0034	0.0044	-0.0117	0.0024	0.0059	0.0059
hour[14-13]	-0.0058	0.0066	-0.0048	0.0033	-0.0015	0.0023	0.0036	0.0042	-0.0012	0.0044	0.0034	0.0024	-0.0131	0.0059
hour[15-14]	-0.0034	0.0066	-0.0062	0.0033	-0.0022	0.0023	-0.0014	0.0042	-0.0030	0.0044	-0.0021	0.0025	0.0061	0.0059
hour[16-15]	-0.0086	0.0066	-0.0020	0.0033	-0.0016	0.0023	0.0025	0.0042	0.0035	0.0044	-0.0004	0.0025	-0.0074	0.0059
hour[17-16]	0.0024	0.0066	-0.0015	0.0033	-0.0014	0.0023	-0.0015	0.0042	-0.0021	0.0044	0.0017	0.0025	0.0057	0.0058
hour[18-17]	-0.0073	0.0066	0.0012	0.0033	0.0038	0.0023	0.0051	0.0043	-0.0036	0.0044	0.0010	0.0025	-0.0083	0.0058
hour[19-18]	-0.0062	0.0066	-0.0004	0.0033	0.0006	0.0023	0.0033	0.0043	-0.0026	0.0044	0.0001	0.0025	0.0041	0.0058
hour[20-19]	-0.0029	0.0066	-0.0003	0.0033	-0.0013	0.0023	-0.0026	0.0042	-0.0044	0.0044	-0.0040	0.0024	0.0135	0.0058
hour[21-20]	-0.0087	0.0066	0.0011	0.0033	0.0021	0.0023	-0.0004	0.0042	0.0001	0.0044	-0.0009	0.0024	-0.0062	0.0058
hour[22-21]	-0.0050	0.0066	-0.0001	0.0033	0.0009	0.0023	0.0003	0.0042	-0.0031	0.0044	-0.0002	0.0024	0.0106	0.0058
hour[23-22]	0.0026	0.0066	-0.0020	0.0033	-0.0043	0.0023	-0.0028	0.0043	0.0005	0.0044	-0.0013	0.0024	-0.0054	0.0057

Table S4: Estimated values of hour effect and standard error, generated from a LME for the response variable fish displacement (body lengths per second, BLs^{-1}) for pelagic charr ecomorphs (*n*=10). Values are given for each photoperiod category (A-D2), intercept hour[0-23].

	A		B1		B2		B3		C		D1		D2	
	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.
Intercept	0.0657	0.0185	0.0301	0.0090	0.0272	0.0131	0.0171	0.0044	0.0251	0.0084	0.0399	0.0143	0.1018	0.0185
hour[1-0]	0.0075	0.0164	0.0027	0.0084	0.0030	0.0050	0.0008	0.0035	0.0045	0.0068	0.0102	0.0059	0.0085	0.0129
hour[2-1]	0.0262	0.0164	0.0010	0.0084	-0.0034	0.0049	-0.0007	0.0035	0.0059	0.0068	-0.0079	0.0058	-0.0251	0.0128
hour[3-2]	0.0499	0.0164	0.0024	0.0084	0.0025	0.0050	0.0004	0.0035	0.0095	0.0068	0.0086	0.0059	0.0192	0.0125
hour[4-3]	0.0165	0.0164	0.0018	0.0084	-0.0006	0.0050	-0.0013	0.0035	0.0024	0.0067	0.0011	0.0060	-0.0083	0.0128
hour[5-4]	0.0080	0.0164	0.0058	0.0084	0.0036	0.0049	-0.0002	0.0035	0.0118	0.0067	-0.0069	0.0061	0.0030	0.0128
hour[6-5]	0.0072	0.0164	0.0108	0.0084	-0.0023	0.0050	-0.0001	0.0035	0.0133	0.0068	0.0066	0.0061	-0.0012	0.0128
hour[7-6]	-0.0246	0.0164	0.0127	0.0084	0.0045	0.0050	0.0047	0.0035	0.0035	0.0068	-0.0017	0.0062	0.0132	0.0127
hour[8-7]	-0.0090	0.0164	0.0031	0.0084	0.0040	0.0050	-0.0003	0.0035	-0.0049	0.0068	0.0055	0.0061	0.0037	0.0126
hour[9-8]	0.0046	0.0164	-0.0030	0.0085	-0.0031	0.0051	-0.0009	0.0035	0.0035	0.0068	0.0001	0.0061	-0.0087	0.0127
hour[10-9]	0.0027	0.0164	-0.0027	0.0084	0.0059	0.0050	0.0028	0.0035	-0.0007	0.0068	-0.0023	0.0060	0.0177	0.0129
hour[11-10]	-0.0007	0.0164	-0.0066	0.0084	-0.0012	0.0050	-0.0004	0.0035	-0.0004	0.0067	0.0158	0.0060	-0.0185	0.0134
hour[12-11]	-0.0111	0.0164	0.0017	0.0084	-0.0039	0.0049	0.0020	0.0035	-0.0108	0.0067	-0.0064	0.0060	0.0012	0.0134
hour[13-12]	0.0041	0.0164	-0.0004	0.0084	0.0031	0.0050	-0.0041	0.0035	-0.0082	0.0068	-0.0120	0.0060	-0.0047	0.0130
hour[14-13]	-0.0070	0.0164	-0.0127	0.0084	-0.0077	0.0050	-0.0020	0.0035	0.0059	0.0067	-0.0050	0.0060	0.0125	0.0129
hour[15-14]	-0.0072	0.0164	-0.0120	0.0084	-0.0032	0.0049	0.0006	0.0035	-0.0063	0.0067	0.0062	0.0060	-0.0148	0.0130
hour[16-15]	-0.0154	0.0164	-0.0049	0.0084	0.0007	0.0050	0.0014	0.0035	-0.0104	0.0067	-0.0028	0.0061	0.0158	0.0132
hour[17-16]	0.0002	0.0164	0.0002	0.0084	-0.0009	0.0050	0.0025	0.0035	0.0011	0.0067	-0.0077	0.0062	-0.0021	0.0132
hour[18-17]	-0.0153	0.0164	0.0035	0.0084	0.0031	0.0050	0.0014	0.0035	-0.0098	0.0067	-0.0003	0.0062	-0.0116	0.0133
hour[19-18]	-0.0063	0.0164	-0.0031	0.0084	-0.0038	0.0050	-0.0032	0.0035	-0.0020	0.0067	0.0007	0.0060	0.0119	0.0130
hour[20-19]	-0.0180	0.0164	-0.0003	0.0084	0.0014	0.0049	-0.0052	0.0035	-0.0037	0.0067	0.0047	0.0061	-0.0222	0.0129
hour[21-20]	-0.0035	0.0164	0.0020	0.0084	0.0005	0.0049	0.0035	0.0035	0.0005	0.0068	-0.0023	0.0061	0.0091	0.0129
hour[22-21]	0.0039	0.0164	-0.0014	0.0084	-0.0031	0.0049	0.0003	0.0035	-0.0013	0.0068	-0.0012	0.0062	0.0214	0.0131
hour[23-22]	-0.0128	0.0164	0.0038	0.0084	0.0085	0.0049	0.0005	0.0035	0.0001	0.0068	-0.0018	0.0062	-0.0212	0.0129

Table S5: Estimated values of hour effect and standard error, generated from a LME for the response variable fish depth (m) for littoral charr ecomorphs (*n*=13). Values are given for each photoperiod category (A-D2), intercept hour[0-23].

	A		B1		C		D1		D2	
	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.
Intercept	8.4078	1.6667	12.4325	2.4976	11.1441	2.3911	10.7329	2.3598	9.5028	1.4821
hour[1-0]	0.1450	0.8666	0.0014	0.3307	0.0935	0.3516	0.0116	0.1637	-0.2521	0.2269
hour[2-1]	-0.0217	0.8670	-0.0975	0.3292	-0.0306	0.3527	0.2076	0.1624	0.3243	0.2281
hour[3-2]	-0.0107	0.8670	-0.0415	0.3297	0.1930	0.3518	0.0105	0.1623	-0.2901	0.2295
hour[4-3]	-0.0575	0.8660	0.0318	0.3306	0.0818	0.3510	0.0325	0.1613	-0.1280	0.2307
hour[5-4]	0.3641	0.8660	-0.0661	0.3306	0.0473	0.3527	0.0586	0.1618	0.0564	0.2311
hour[6-5]	-0.1399	0.8660	0.0954	0.3301	0.0544	0.3540	0.0496	0.1617	-0.0995	0.2315
hour[7-6]	0.1028	0.8670	0.1176	0.3311	0.3414	0.3523	-0.1056	0.1621	-0.4120	0.2329
hour[8-7]	0.1032	0.8660	0.2120	0.3311	0.1651	0.3514	-0.0595	0.1621	0.2749	0.2339
hour[9-8]	0.1064	0.8650	-0.0651	0.3301	0.0445	0.3518	-0.0279	0.1606	0.1794	0.2331
hour[10-9]	-0.0025	0.8649	0.2087	0.3297	-0.0346	0.3531	0.3110	0.1612	-0.0556	0.2336
hour[11-10]	-0.0456	0.8649	-0.0465	0.3306	-0.0745	0.3523	0.0302	0.1611	0.0821	0.2332
hour[12-11]	-0.0869	0.8649	-0.0180	0.3316	-0.1363	0.3502	0.1992	0.1598	0.2067	0.2320
hour[13-12]	0.1605	0.8649	-0.2365	0.3306	-0.2468	0.3510	0.0541	0.1597	-0.2114	0.2298
hour[14-13]	-0.3427	0.8649	0.0127	0.3311	-0.1989	0.3518	-0.1849	0.1608	-0.1372	0.2304
hour[15-14]	0.1469	0.8649	-0.1645	0.3320	-0.1594	0.3514	-0.3454	0.1620	0.0233	0.2298
hour[16-15]	-0.0158	0.8650	0.1520	0.3316	0.0124	0.3519	0.0006	0.1628	-0.3917	0.2298
hour[17-16]	-0.0036	0.8660	-0.1645	0.3316	0.0531	0.3540	-0.0972	0.1622	-0.2101	0.2279
hour[18-17]	0.1134	0.8660	0.0235	0.3316	-0.2428	0.3540	0.1983	0.1627	0.1674	0.2279
hour[19-18]	-0.1305	0.8660	-0.0172	0.3316	0.2187	0.3527	-0.2974	0.1625	0.2941	0.2284
hour[20-19]	-0.1648	0.8670	0.0027	0.3320	-0.1842	0.3531	-0.0078	0.1606	0.0950	0.2283
hour[21-20]	0.0562	0.8670	-0.0031	0.3316	0.0474	0.3523	0.0435	0.1599	0.4174	0.2289
hour[22-21]	-0.0314	0.8670	0.0426	0.3306	-0.0057	0.3523	-0.0913	0.1594	0.3943	0.2279
hour[23-22]	-0.1015	0.8676	0.0187	0.3316	-0.0480	0.3524	-0.0579	0.1606	-0.0504	0.2258

Table S6: Estimated values of hour effect and standard error, generated from a LME for the response variable fish depth (m) for pelagic charr ecomorphs (*n*=10). Values are given for each photoperiod category (A-D2), intercept hour[0-23].

	A		B1		C		D1		D2	
	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.	Est.	S.E.
Intercept	9.4700	1.5600	11.2803	1.3153	12.1577	1.4568	13.4089	2.0798	21.2061	2.2001
hour[1-0]	0.2735	1.2670	0.0330	0.4929	-0.4352	0.6036	0.2277	0.1589	0.8003	0.3622
hour[2-1]	-0.2699	1.2660	-0.0813	0.4919	0.1148	0.6012	0.3079	0.1573	0.0887	0.3587
hour[3-2]	0.6866	1.2659	0.0489	0.4935	0.0794	0.5992	0.1821	0.1585	-0.2181	0.3587
hour[4-3]	0.6128	1.2659	0.0320	0.4935	0.1017	0.5981	0.0887	0.1602	0.1545	0.3612
hour[5-4]	0.0747	1.2660	0.0088	0.4919	0.1395	0.5971	-0.2655	0.1623	-0.3980	0.3613
hour[6-5]	0.1072	1.2680	-0.0985	0.4935	0.7955	0.5992	0.0300	0.1627	-0.4126	0.3621
hour[7-6]	0.0941	1.2699	-0.0484	0.4951	0.5946	0.6012	-0.2134	0.1657	0.2175	0.3567
hour[8-7]	0.0768	1.2680	-0.1717	0.4960	0.3544	0.6002	0.0421	0.1635	-0.2307	0.3559
hour[9-8]	-0.1924	1.2680	0.1404	0.4985	-0.0062	0.6012	-0.1759	0.1621	-0.0461	0.3607
hour[10-9]	0.0456	1.2679	-0.0345	0.4969	0.3093	0.6012	-0.0894	0.1620	0.3259	0.3605
hour[11-10]	-0.1283	1.2660	0.0921	0.4927	-0.6664	0.5972	0.0115	0.1603	-0.4577	0.3702
hour[12-11]	0.2261	1.2659	-0.0359	0.4927	0.4316	0.5972	0.0233	0.1604	0.1292	0.3700
hour[13-12]	0.4984	1.2659	0.0402	0.4943	-0.8074	0.6002	0.4703	0.1603	-0.2272	0.3615
hour[14-13]	-0.4479	1.2659	-0.0308	0.4935	-0.2751	0.5982	-0.0407	0.1608	-0.0342	0.3642
hour[15-14]	0.1987	1.2660	0.1818	0.4911	-0.3845	0.5961	-0.1007	0.1609	0.2672	0.3656
hour[16-15]	-0.4175	1.2679	-0.0946	0.4919	-0.1937	0.5981	-0.2382	0.1637	0.3453	0.3678
hour[17-16]	0.1558	1.2679	0.0424	0.4927	-0.4870	0.5971	-0.1456	0.1635	-0.2910	0.3662
hour[18-17]	-0.1833	1.2660	0.0049	0.4927	0.0768	0.5971	0.1069	0.1645	-0.1744	0.3705
hour[19-18]	-0.2024	1.2659	-0.0296	0.4927	-0.1764	0.5981	-0.0382	0.1618	0.1349	0.3629
hour[20-19]	-0.8389	1.2659	-0.0524	0.4911	0.1905	0.5982	0.0461	0.1619	-0.7380	0.3618
hour[21-20]	-0.2434	1.2659	0.2002	0.4910	-0.3052	0.6012	0.1372	0.1627	-0.0277	0.3627
hour[22-21]	0.0294	1.2660	-0.1661	0.4919	0.2384	0.6002	-0.1274	0.1634	0.6291	0.3660
hour[23-22]	-0.0543	1.2670	0.0426	0.4929	-0.3359	0.5996	0.0389	0.1660	0.0865	0.3669

Table S7: Welch *ANOVA* outputs for the response variable fish displacement (BLs^{-1}) with predictor hour-of-day (23 *df*), for each charr individual and each photoperiod category (A-D2). Where insufficient data were available, N/A is stated. Power simulations based upon parametric resampling were performed; values are stated (π). Fish 1-13 are littoral morph fish, fish 14-23 pelagic. Bonferroni correction was applied (adjusted significance level p = 0.002, indicated as an asterisk when significant), hourly 95% confidence limits were calculated and presented in the supplementary figures.

Category of photoperiod	Fish ID	F	df Den	p	π
A		38.8125	741.6620	<0.0001 *	1.000
B1		8.1793	391.3488	<0.0001 *	1.000
B2		2.7300	331.2078	<0.0001 *	0.996
B3	Fish 1	1.7671	124.5447	0.0253	0.827
C		16.7845	990.7668	<0.0001 *	1.000
D1		1.2383	242.0668	0.2130	0.578
D2		1.3271	562.8634	0.1417	0.647
A		1.8305	537.8601	0.0109	0.893
B1		4.9767	275.1682	<0.0001 *	1.000
B2		1.5047	194.3366	0.0723	0.743
B3	Fish 2	2.0489	80.0375	0.0101	0.912
C		6.5513	713.6694	<0.0001 *	1.000
D1		1.6463	183.6913	0.0380	0.788
D2		1.4241	253.8473	0.0990	0.678
A		12.9965	695.3854	<0.0001 *	1.000
B1		8.4362	321.6754	<0.0001 *	1.000
B2		1.3967	296.3607	0.1096	0.692
B3	Fish 3	N/A			
C		46.6336	853.7830	<0.0001 *	1.000
D1		1.2760	238.0514	0.1845	0.601
D2		1.6831	573.0204	0.0246	0.841
A		34.5011	735.5468	<0.0001 *	1.000
B1		2.9589	263.4622	<0.0001 *	0.997
B2		3.2827	268.2331	<0.0001 *	1.000
B3	Fish 4	N/A			
C		4.2708	640.5082	<0.0001 *	1.000
D1		N/A			
D2		N/A			

Category of photoperiod	Fish ID	*F*	*df* Den	*p*	*π*
A	Fish 5	3.4497	664.0252	<0.0001 *	1.000
B1		2.1241	346.1249	0.0022	0.941
B2		1.9836	246.1895	0.0059	0.927
B3		0.7955	105.1760	0.7299	0.259
C		17.3553	831.4487	<0.0001 *	1.000
D1		0.7130	187.3192	0.8291	0.187
D2		5.8859	206.4974	<0.0001 *	1.000
A	Fish 6	7.7121	520.8762	<0.0001 *	1.000
B1		1.9546	237.3294	0.0070	0.911
B2		1.9892	155.7522	0.0075	0.931
B3		N/A			
C		14.0863	780.7416	<0.0001 *	1.000
D1		2.7238	112.8596	0.0002 *	0.986
D2		2.6354	329.0867	<0.0001 *	0.988
A	Fish 7	10.3717	611.0215	<0.0001 *	1.000
B1		5.1390	308.3813	<0.0001 *	1.000
B2		3.9558	281.1403	<0.0001 *	1.000
B3		1.3410	99.4736	0.1617	0.595
C		2.6850	802.2072	<0.0001 *	0.991
D1		1.1484	186.6225	0.2978	0.505
D2		1.7656	545.1329	0.0157	0.886
A	Fish 8	7.6300	723.5523	<0.0001 *	1.000
B1		2.6821	399.1456	0.0001 *	0.990
B2		2.7830	336.6799	<0.0001 *	0.994
B3		1.3151	112.5582	0.1738	0.616
C		13.5017	961.2927	<0.0001 *	1.000
D1		3.7911	214.7690	<0.0001 *	1.000
D2		4.6411	748.9047	<0.0001 *	1.000
A	Fish 9	8.5232	678.4272	<0.0001 *	1.000
B1		8.7402	328.3372	<0.0001 *	1.000
B2		2.0186	239.0293	0.0049	0.927
B3		0.8209	93.4536	0.6976	0.287
C		11.1893	733.3320	<0.0001 *	1.000
D1		1.4127	199.4655	0.1076	0.684
D2		1.1113	156.8361	0.3388	0.475

Category of photoperiod	Fish ID	F	df Den	p	π
A		19.7210	591.3423	<0.0001 *	1.000
B1		6.2833	289.2912	<0.0001 *	1.000
B2		1.5703	216.7680	0.0522	0.778
B3	Fish 10	1.0598	96.4339	0.4034	0.411
C		21.5763	792.8364	<0.0001 *	1.000
D1		1.0067	176.1688	0.4594	0.388
D2		1.6074	586.2534	0.0368	0.800
A		16.8488	631.2482	<0.0001 *	1.000
B1		5.7809	263.3221	<0.0001 *	1.000
B2		3.4496	240.1522	<0.0001 *	0.999
B3	Fish 11	N/A			
C		33.8914	671.1527	<0.0001 *	1.000
D1		2.0481	182.2982	0.0049	0.922
D2		2.1989	604.3354	0.0011 *	0.951
A		7.0643	715.9239	<0.0001 *	1.000
B1		1.9103	317.6356	0.0080	0.910
B2		4.5749	253.6985	<0.0001 *	1.000
B3	Fish 12	1.3775	55.2533	0.1652	0.635
C		5.8383	352.2732	<0.0001 *	1.000
D1		N/A			
D2		5.4183	532.3787	<0.0001 *	1.000
A		9.8890	667.1307	<0.0001 *	1.000
B1		7.8040	356.1513	<0.0001 *	1.000
B2		0.9405	209.4917	0.5445	0.371
B3	Fish 13	0.5762	96.9063	0.9344	0.152
C		9.3449	806.1942	<0.0001 *	1.000
D1		1.6200	215.7337	0.0412	0.805
D2		0.8019	185.4604	0.7265	0.259

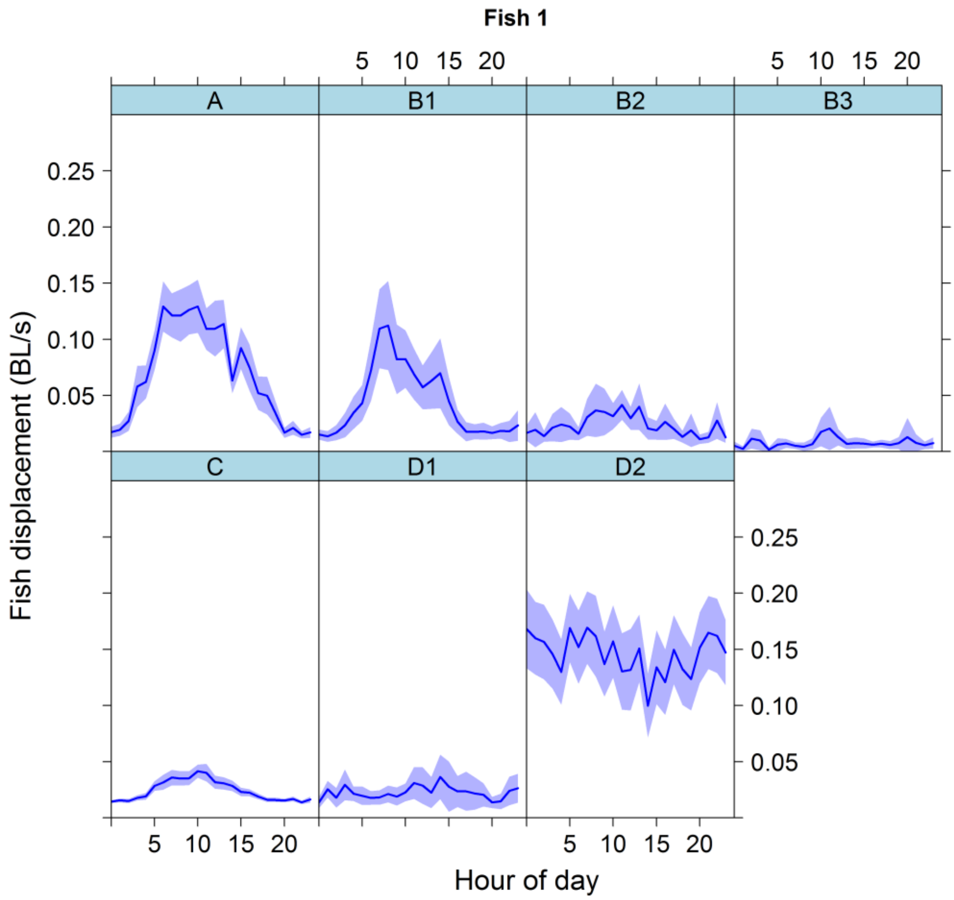
Category of photoperiod	Fish ID	*F*	*df* Den	*p*	*π*
A	Fish 14	12.6417	733.0367	<0.0001 *	1.000
B1		6.8105	360.6786	<0.0001 *	1.000
B2		1.0454	328.9311	0.4072	0.414
B3		0.9504	98.4995	0.5342	0.317
C		27.1084	950.4367	<0.0001 *	1.000
D1		3.1626	240.5691	<0.0001 *	0.999
D2		1.6864	90.1534	0.0430	0.799
A	Fish 15	8.7644	389.6029	<0.0001 *	1.000
B1		7.6983	284.7996	<0.0001 *	1.000
B2		3.6353	230.7562	<0.0001 *	1.000
B3		2.1702	74.1070	0.0066	0.935
C		N/A			
D1		N/A			
D2		N/A			
A	Fish 16	8.4885	710.4896	<0.0001 *	1.000
B1		7.5218	344.9057	<0.0001 *	1.000
B2		1.4739	304.2301	0.0771	0.753
B3		0.9796	85.2507	0.4991	0.372
C		20.3462	880.2496	<0.0001 *	1.000
D1		1.5498	243.1818	0.0561	0.752
D2		0.6463	501.4255	0.8963	0.155
A	Fish 17	39.2473	757.3803	<0.0001 *	1.000
B1		11.2327	379.2809	<0.0001 *	1.000
B2		1.9584	384.7224	0.0056	0.914
B3		0.7700	142.0166	0.7632	0.238
C		30.3257	667.6151	<0.0001 *	1.000
D1		N/A			
D2		N/A			
A	Fish 18	7.0324	613.7663	<0.0001 *	1.000
B1		5.4553	218.7568	<0.0001 *	1.000
B2		1.2579	149.1443	0.2064	0.543
B3		1.2200	70.0377	0.2584	0.484
C		16.4022	653.2705	<0.0001 *	1.000
D1		1.2244	132.9148	0.2353	0.546
D2		2.2611	23.7282	0.0285	

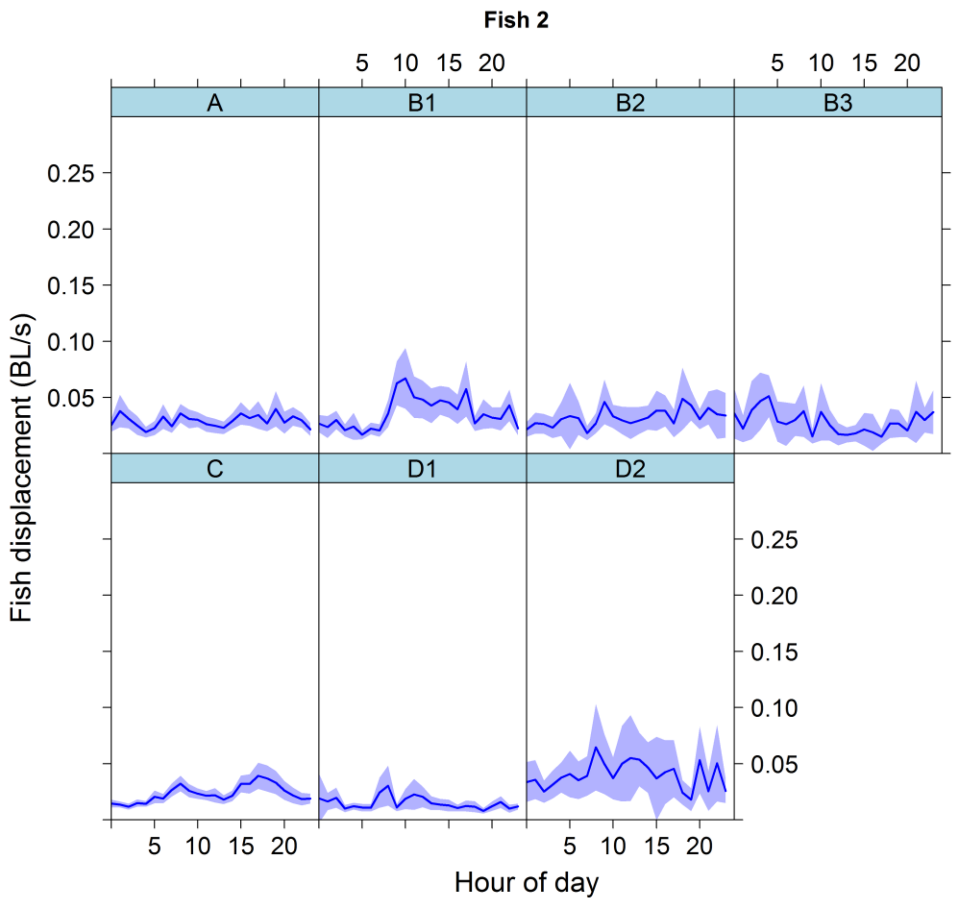
Category of photoperiod	Fish ID	*F*	*df* Den	*p*	π
A		8.2852	744.3454	<0.0001 *	1.000
B1		2.7295	362.1936	<0.0001 *	0.989
B2		2.1276	295.8766	0.0023	0.937
B3	Fish 19	0.9658	66.0542	0.5180	0.374
C		1.9117	708.8075	0.0064	0.905
D1		1.9083	204.1163	0.0097	0.900
D2		1.4032	419.9261	0.1030	0.680
A		14.8159	646.8509	<0.0001 *	1.000
B1		8.4625	332.2673	<0.0001 *	1.000
B2		1.5871	147.6911	0.0536	0.765
B3	Fish 20	N/A			
C		8.6392	816.1629	<0.0001 *	1.000
D1		1.8082	180.2067	0.0173	0.879
D2		2.5549	115.6852	0.0006 *	0.980
A		3.8992	664.8595	<0.0001 *	0.999
B1		4.6981	317.4549	<0.0001 *	1.000
B2		1.2292	278.1275	0.2186	0.565
B3	Fish 21	0.8197	88.8190	0.6987	0.291
C		15.3341	778.4542	<0.0001 *	1.000
D1		2.4669	211.9906	0.0004 *	0.980
D2		1.0686	327.8895	0.3793	0.457
A		12.7627	655.5499	<0.0001 *	1.000
B1		6.2422	227.8794	<0.0001 *	1.000
B2		0.8470	159.7520	0.6680	0.316
B3	Fish 22	0.7310	64.6702	0.7965	0.227
C		5.8897	742.6640	<0.0001 *	1.000
D1		1.9261	147.3989	0.0107	0.884
D2		N/A			
A		8.9047	680.3825	<0.0001 *	1.000
B1		6.6756	315.5817	<0.0001 *	1.000
B2		1.1961	277.1639	0.2472	0.561
B3	Fish 23	0.9956	82.4518	0.4802	0.402
C		7.2144	791.7514	<0.0001 *	1.000
D1		1.3158	199.0944	0.1604	0.614
D2		N/A			

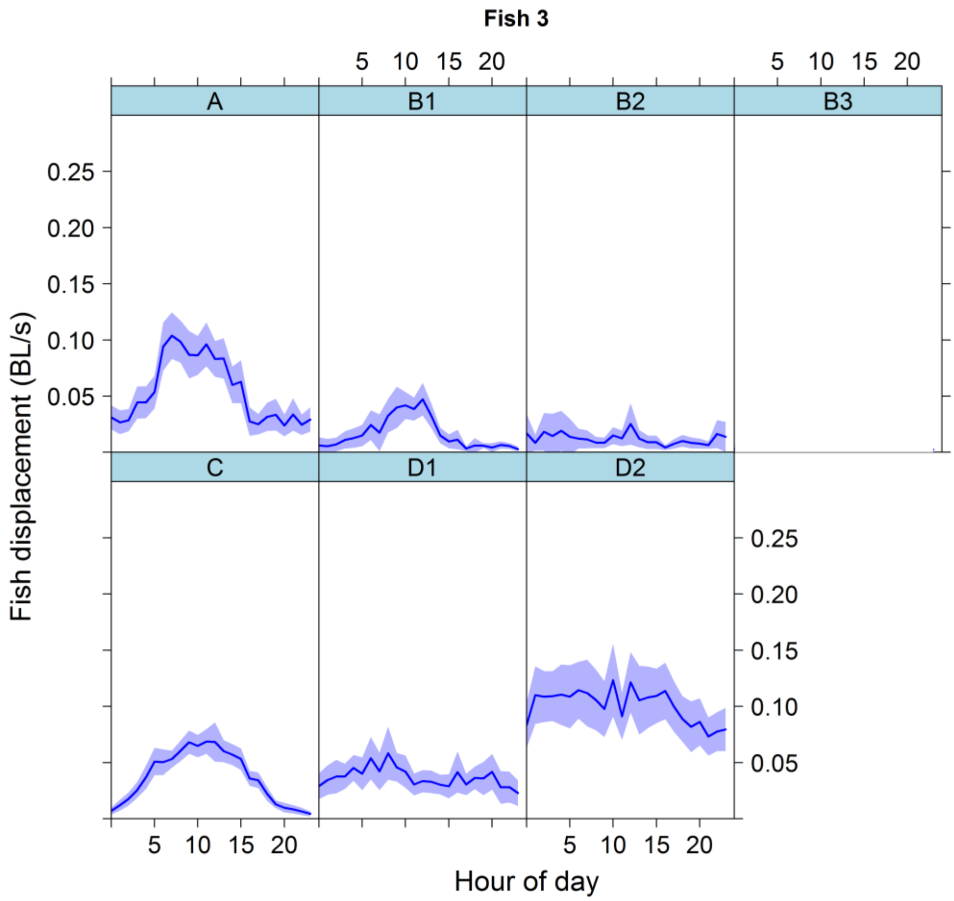
Table S8: Results of Welch ANOVA outputs summarised by Lake Ellasjøen Arctic charr ecomorph, littoral or pelagic. Welch tests were conducted with the response variable fish displacement (BLs^{-1}) with predictor hour of day (23 *df*), for each charr individual and each photoperiod category (A-D2) total *n*=162,530. Bonferroni correction was applied (adjusted significance level p = 0.002), hourly 95% confidence limits were calculated and presented in the supplementary figures.

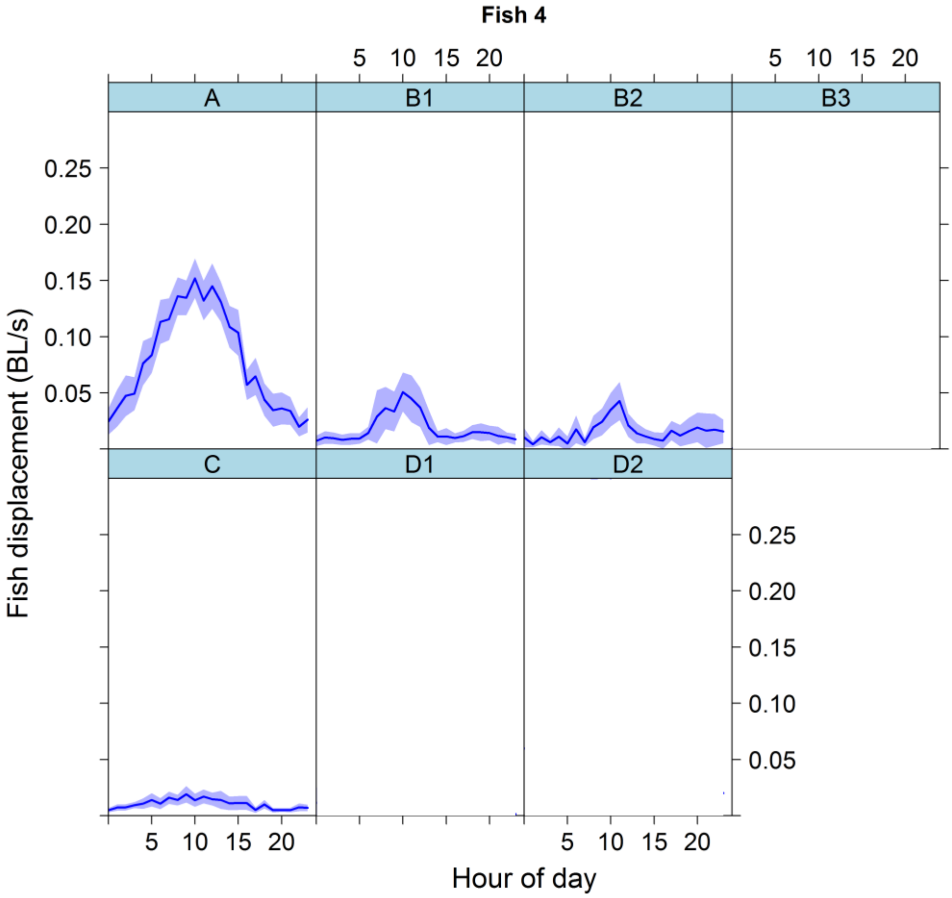
		Significant		Non-significant		
Morph	Photoperiod	n	%	n	%	Total fish
Littoral	A	12	92.31	1	7.69	13
	B1	10	76.92	3	23.08	13
	B2	6	46.15	7	53.85	13
	B3	0	0.00	9	100.00	9
	C	13	100.00	0	0.00	13
	D1	2	18.18	9	81.82	11
	D2	5	41.67	7	58.33	12
Pelagic	A	10	100.00	0	0.00	10
	B1	10	100.00	0	0.00	10
	B2	1	10.00	9	90.00	10
	B3	0	0.00	9	100.00	9
	C	8	88.89	1	11.11	9
	D1	2	25.00	6	75.00	8
	D2	1	16.67	5	83.33	6

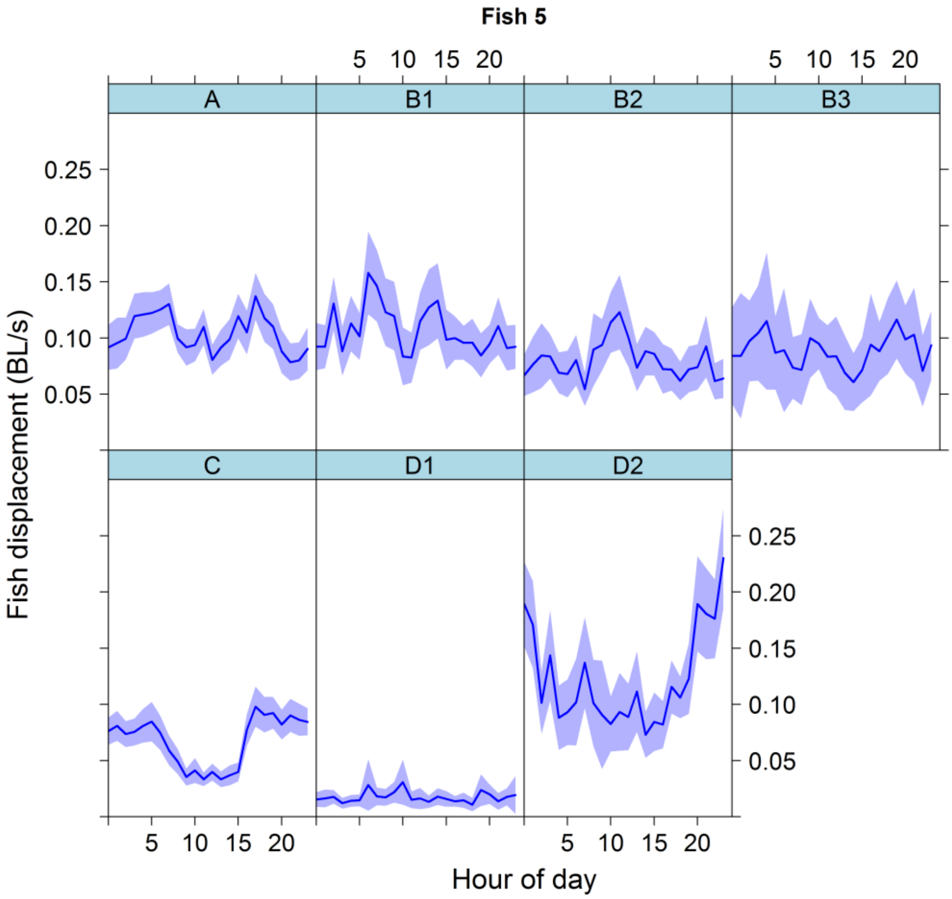
Individual figures of hourly (0-23) mean values of fish displacement (BLs^{-1}) and 95% confidence limits for each category of photoperiod (A-D2), derived from tracking data of Lake Ellasjøen Arctic charr. Fish 1-13 are littoral morph fish (blue), fish 14-23 pelagic (red). Where blank panels are presented, insufficient data were available to perform Welch tests, *df*Den are stated in table S6.

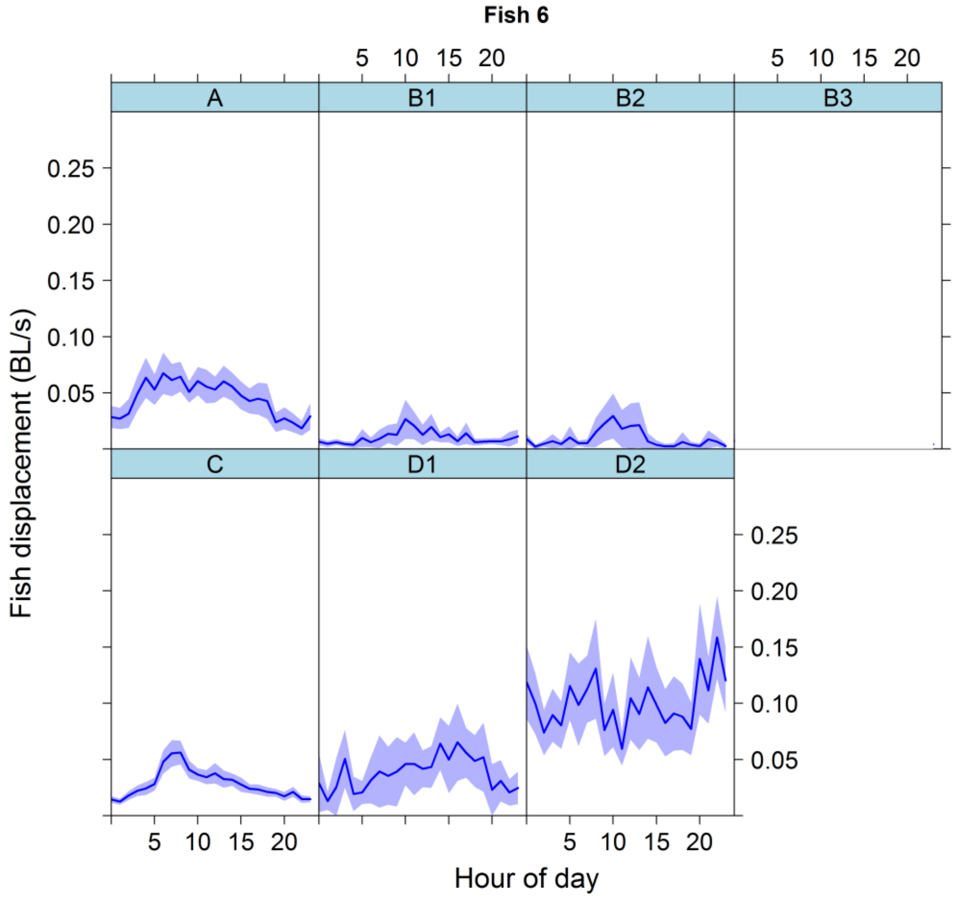


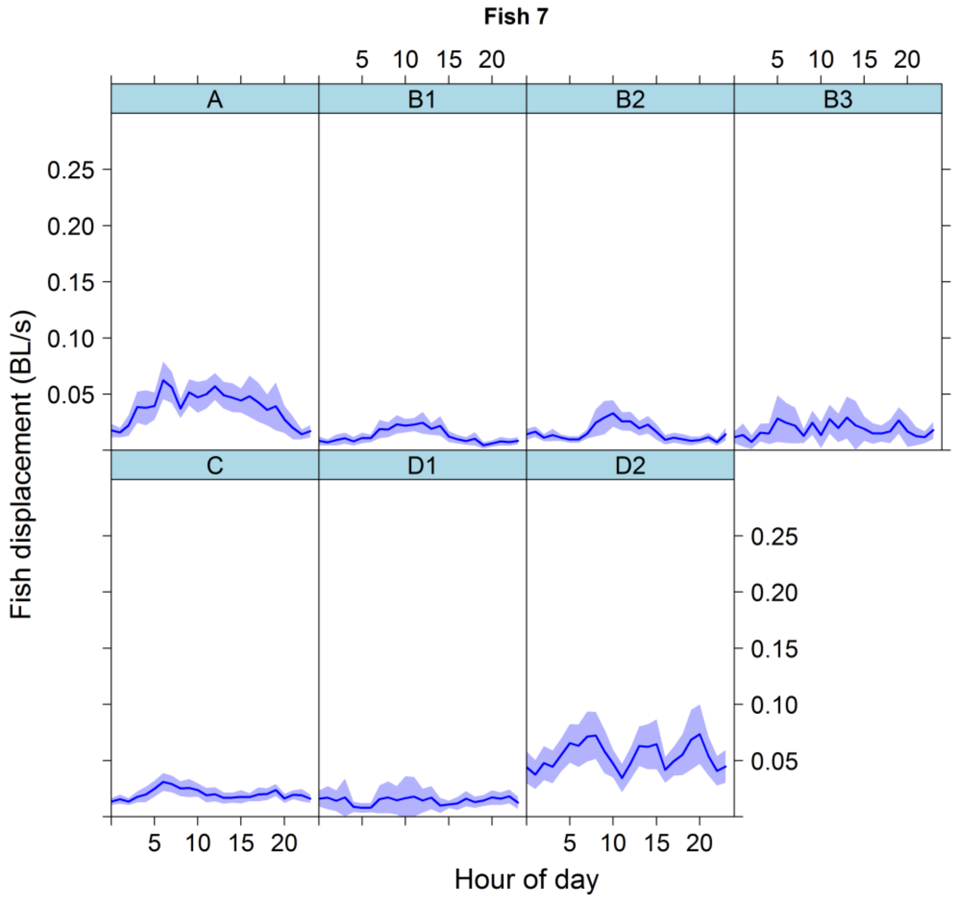

Fish 2
A
B1
B2
B3
C
D1
D2
0.25
0.20
0.15
0.10
0.05
5
10
15
20
Fish displacement (BL/s)
Hour of day

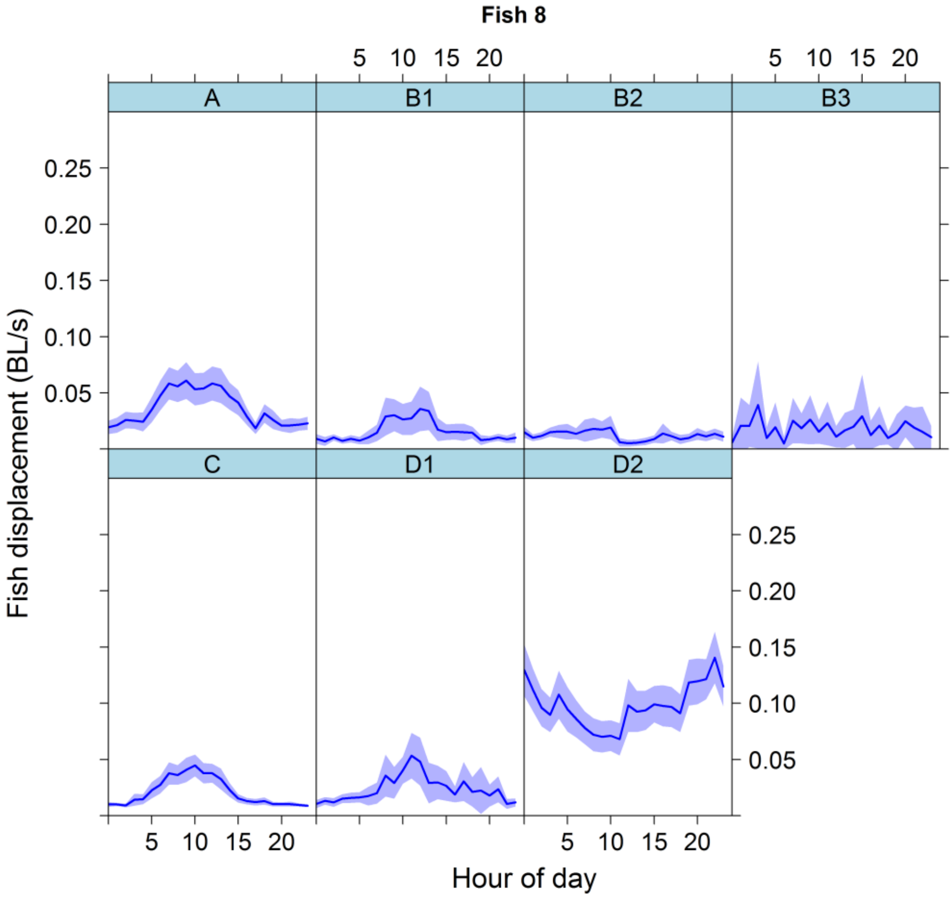

Fish 3
A
B1
B2
B3
C
D1
D2
0.25
0.20
0.15
0.10
0.05
5
10
15
20
Fish displacement (BL/s)
Hour of day


Fish 4
A
B1
B2
B3
C
D1
D2
0.25
0.20
0.15
0.10
0.05
5 10 15 20
Fish displacement (BL/s)
Hour of day

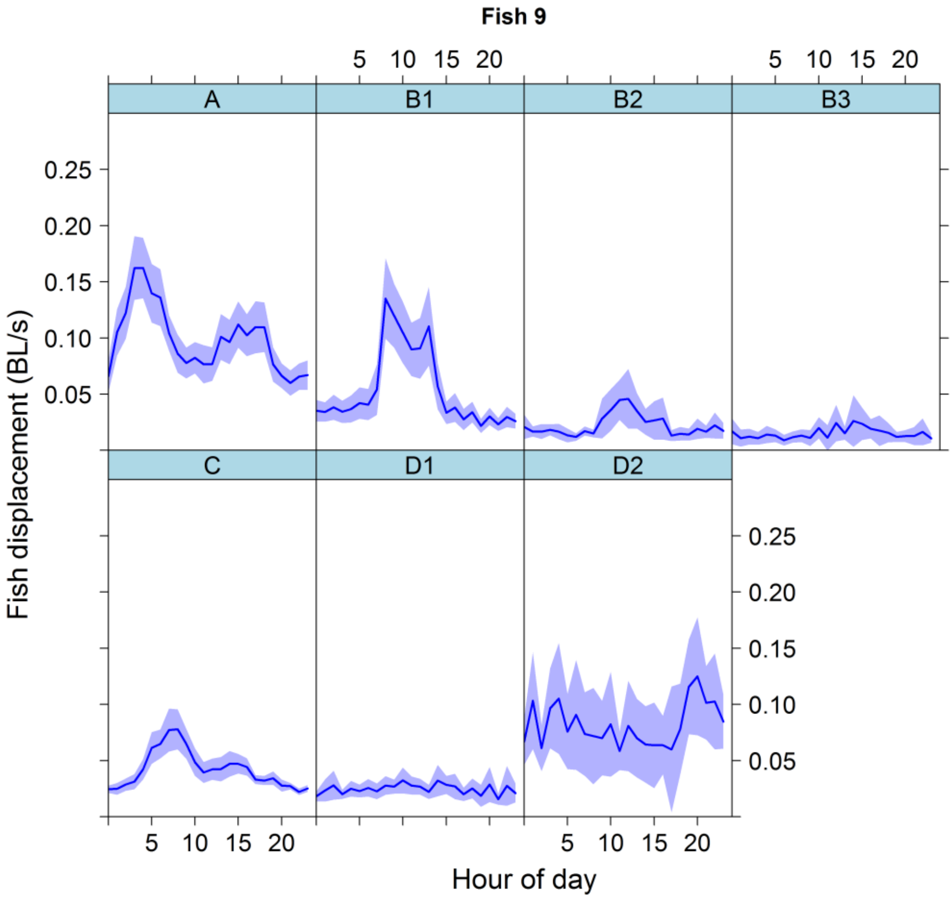

Fish 5
A
B1
B2
B3
C
D1
D2
0.25
0.20
0.15
0.10
0.05
5 10 15 20
Fish displacement (BL/s)
Hour of day


Fish 6
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.25
0.20
0.15
0.10
0.05
5 10 15 20
Hour of day

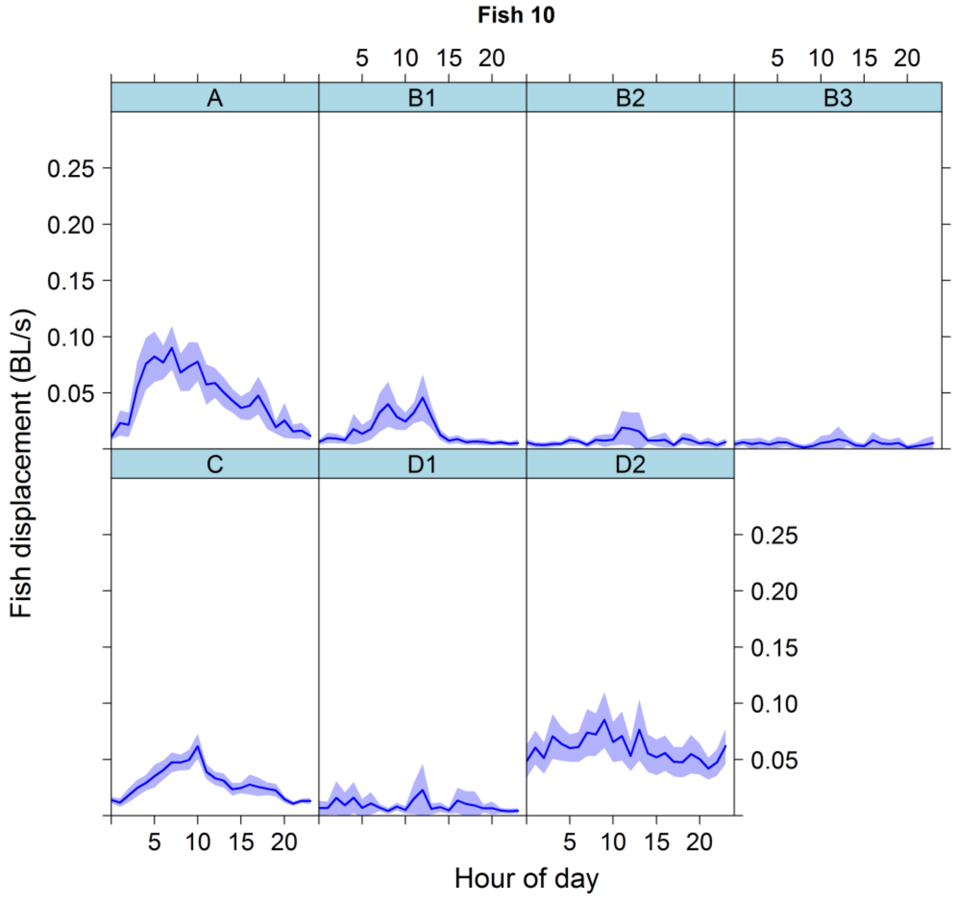

Fish 7
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.25
0.20
0.15
0.10
0.05
5 10 15 20
Hour of day

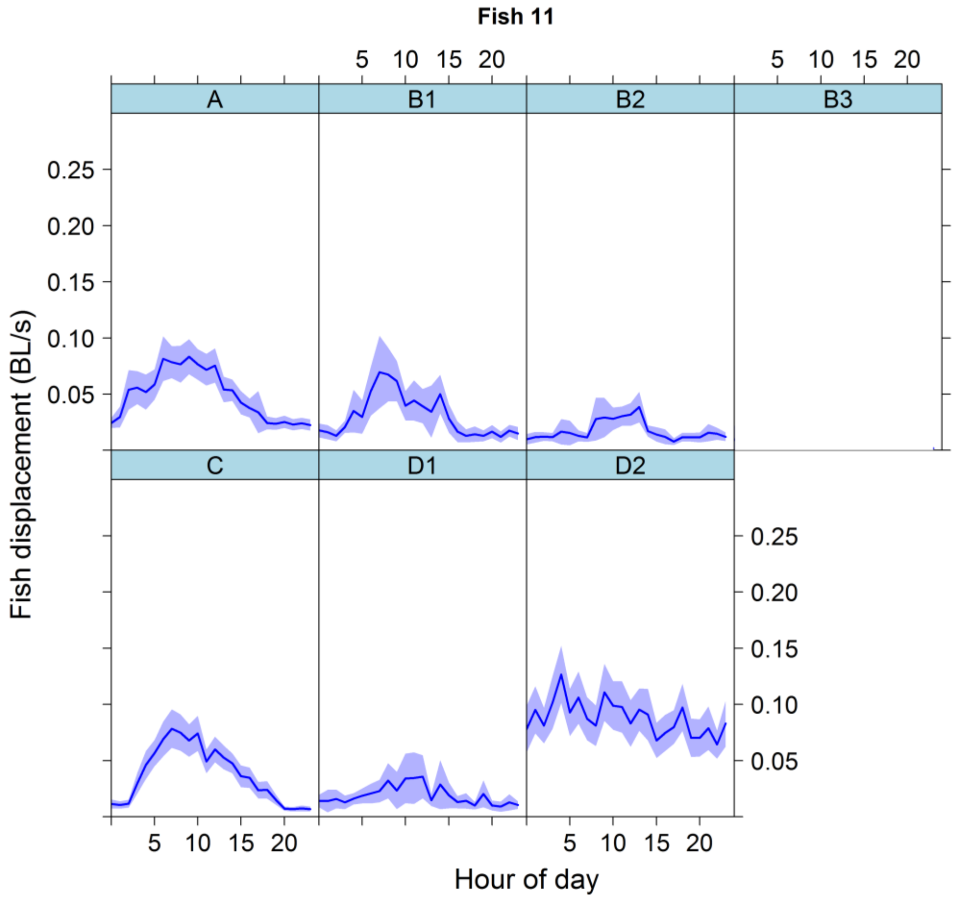

Fish 8
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.25
0.20
0.15
0.10
0.05
5 10 15 20
Hour of day

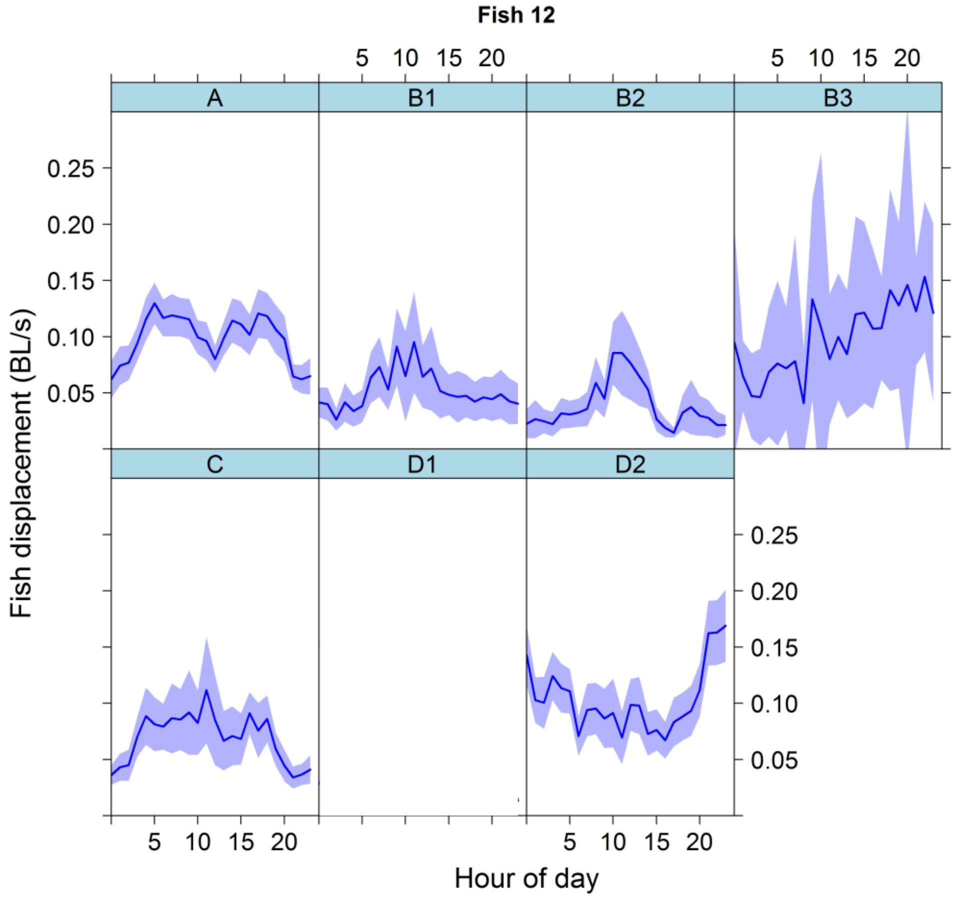
46

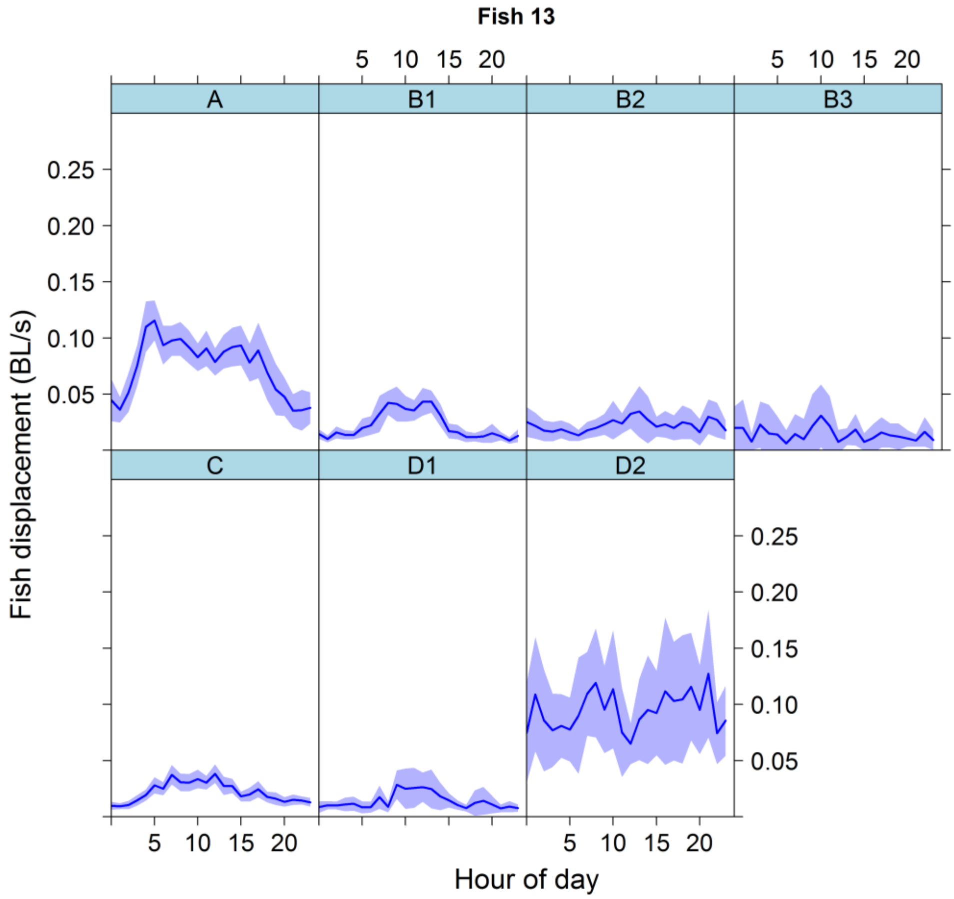

Fish 9
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.25
0.20
0.15
0.10
0.05
5 10 15 20
Hour of day

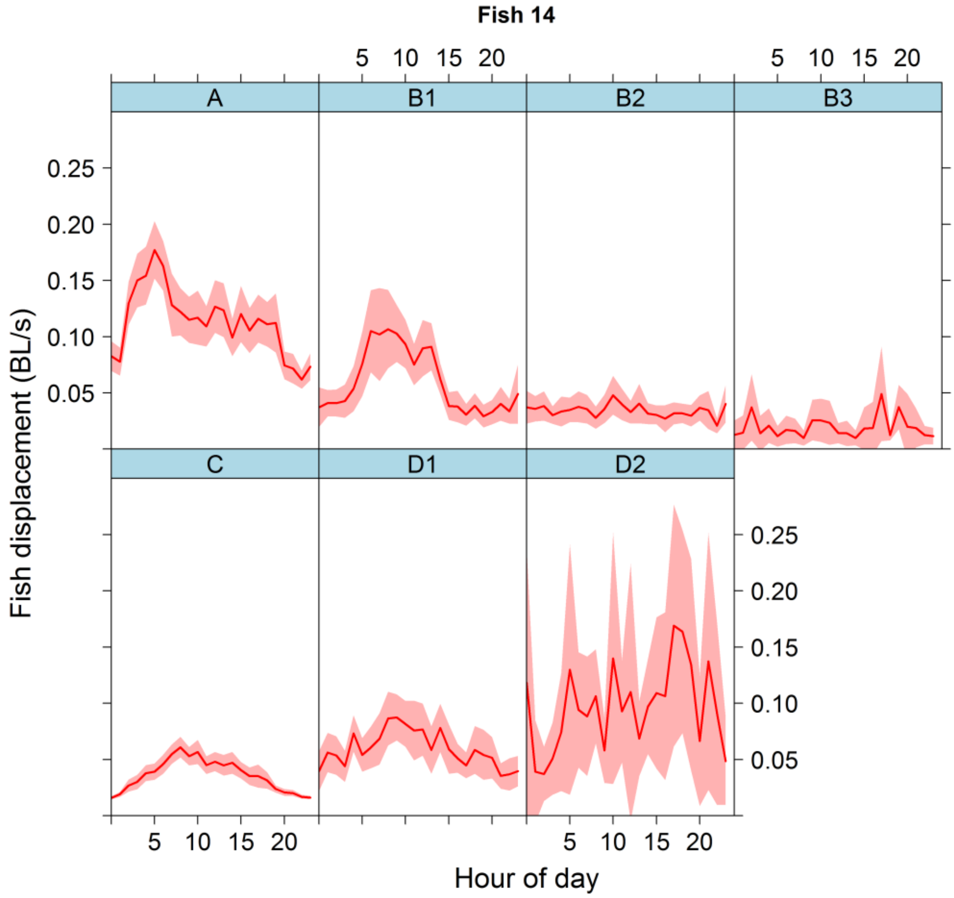
47


Fish 10
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.05
0.10
0.15
0.20
0.25
5
10
15
20
Hour of day


Fish 11
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.05
0.10
0.15
0.20
0.25
5
10
15
20
Hour of day

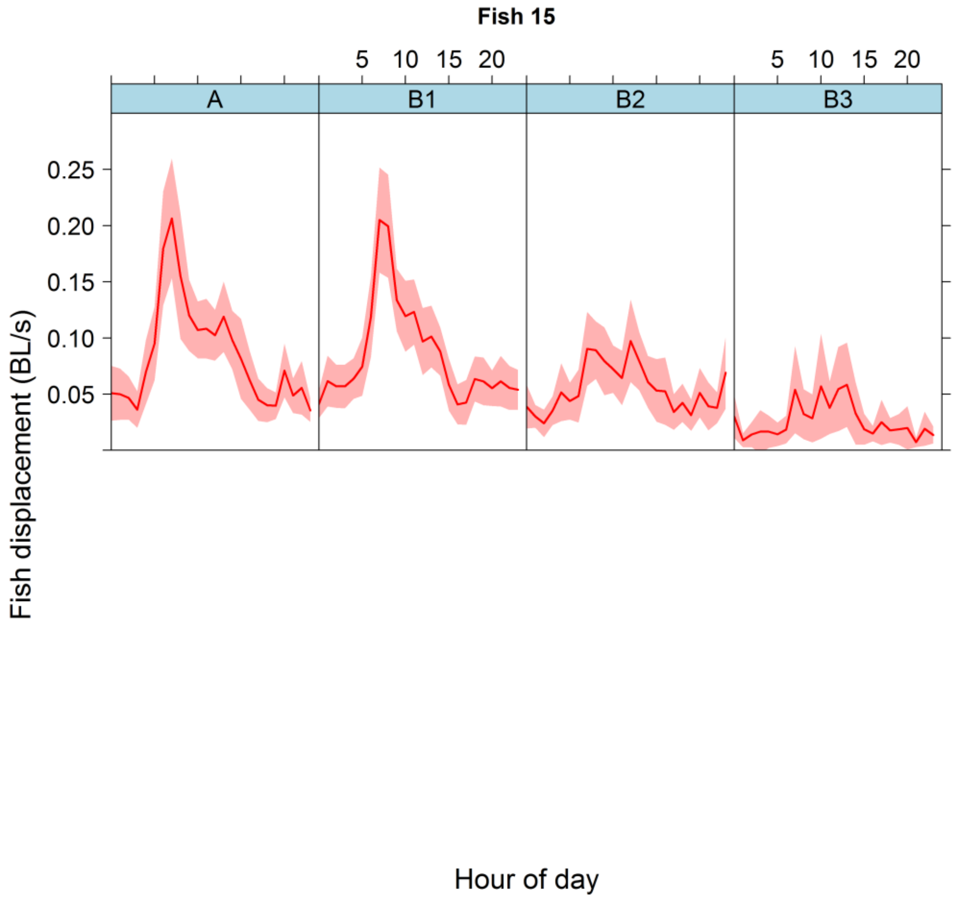

Fish 12
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.05
0.10
0.15
0.20
0.25
5
10
15
20
Hour of day


Fish 13
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.05
0.10
0.15
0.20
0.25
5
10
15
20
Hour of day



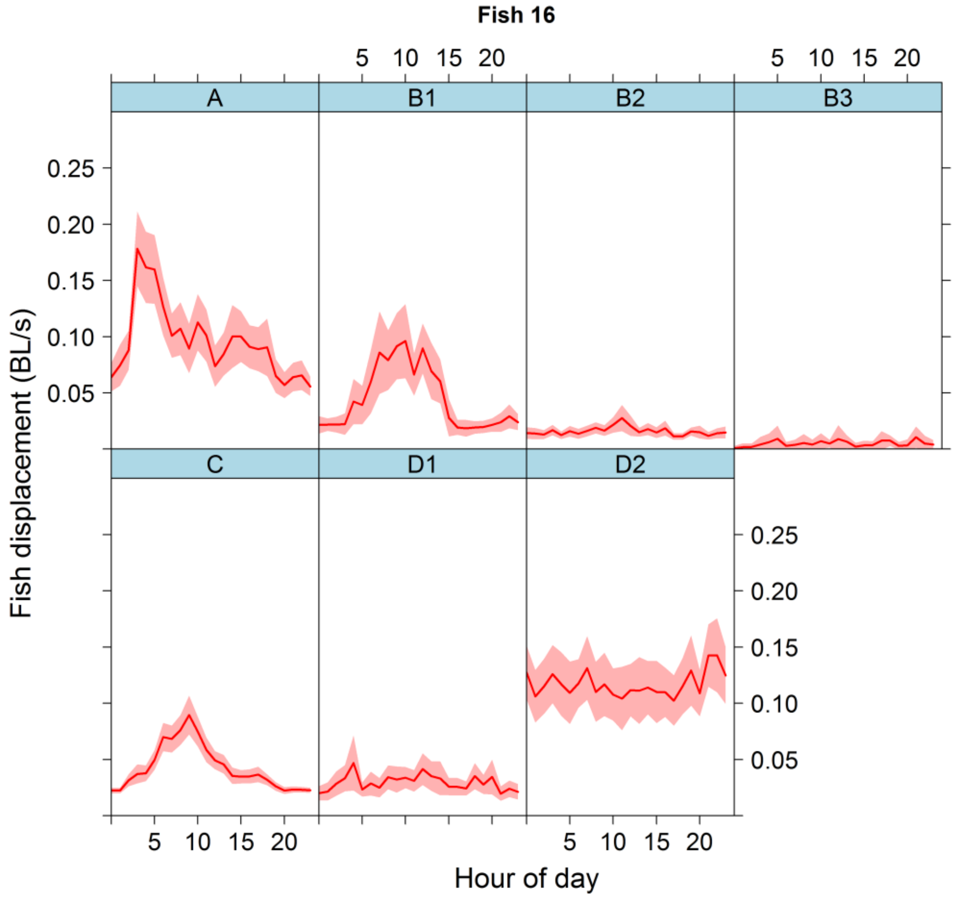
Fish 14
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
Hour of day

53

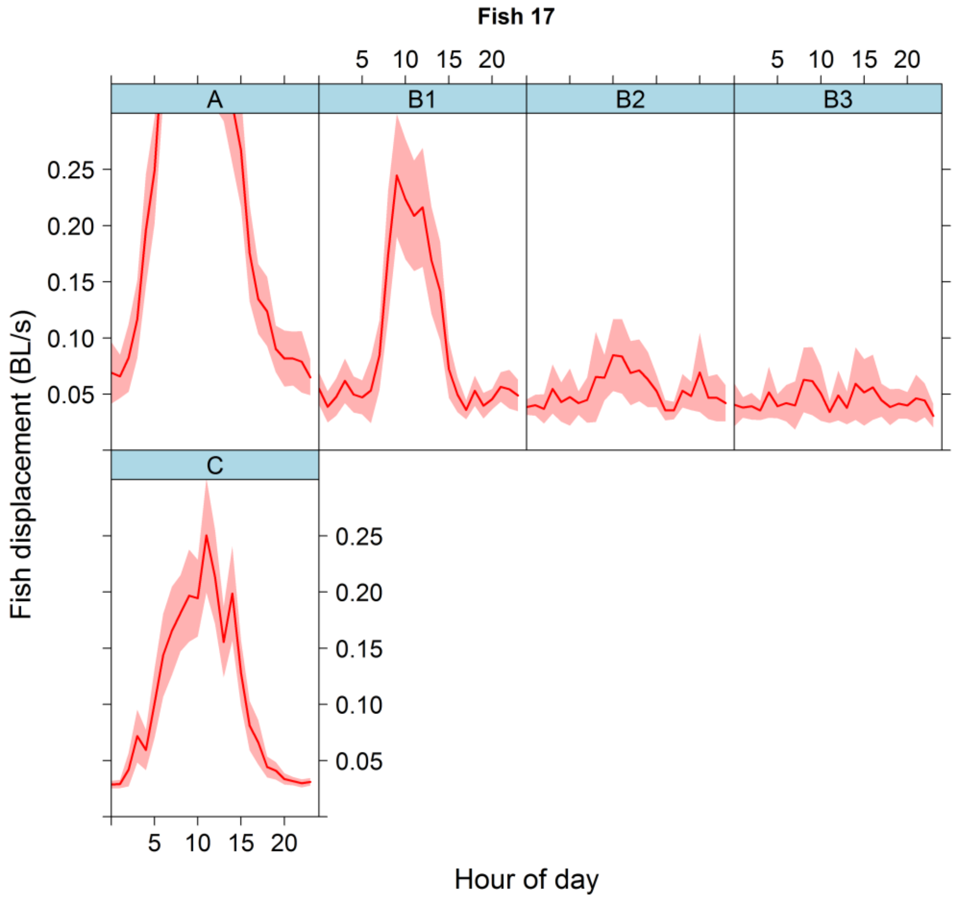


Fish 15
A
B1
B2
B3
Fish displacement (BL/s)
Hour of day

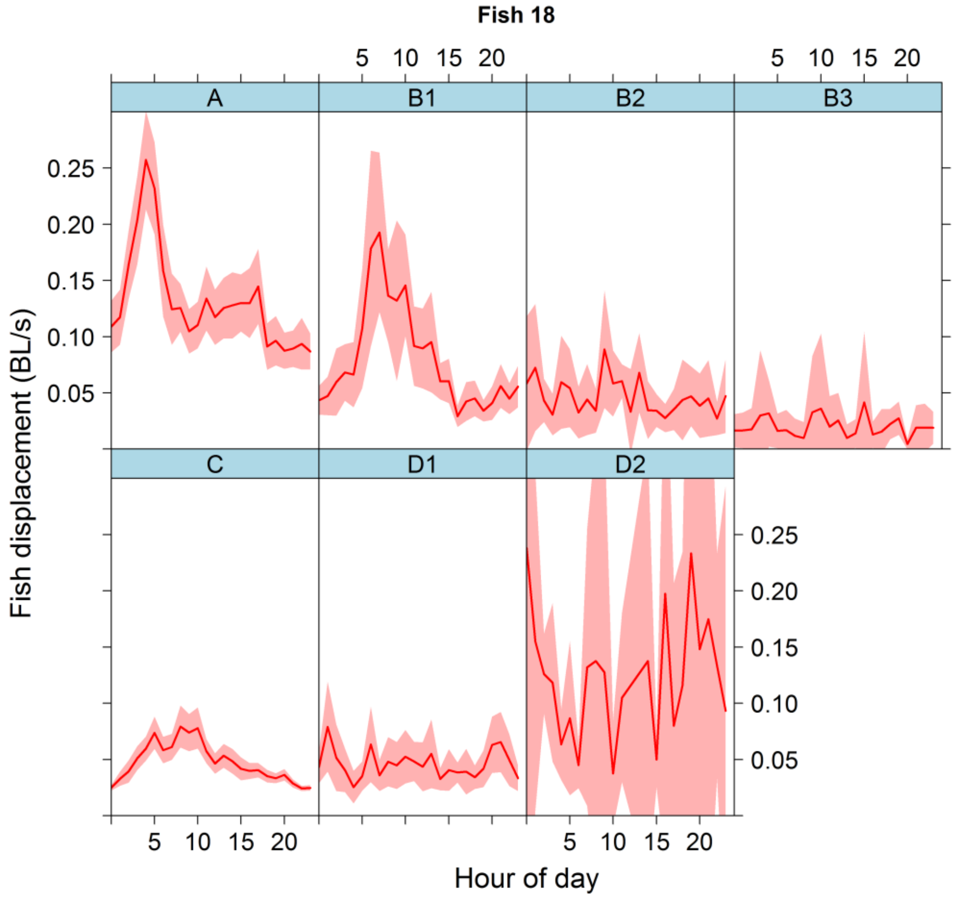
54

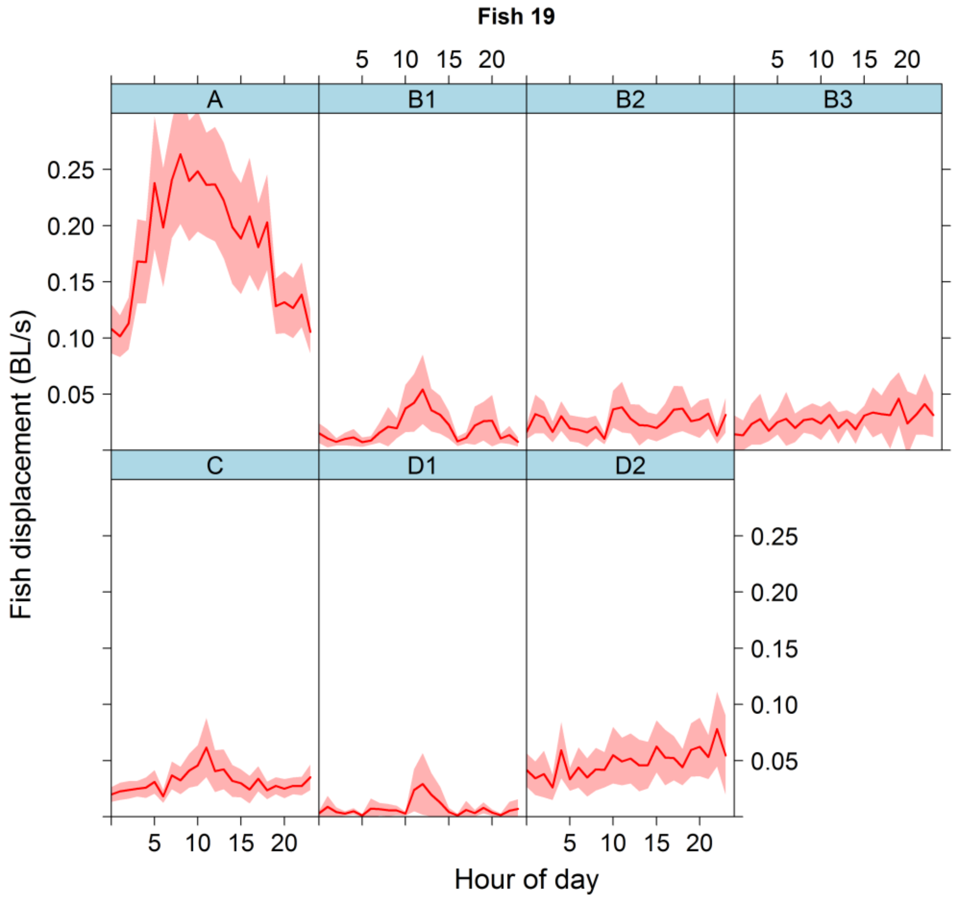

Fish 16
A
B1
B2
B3
C
D1
D2
0.25
0.20
0.15
0.10
0.05
5
10
15
20
Fish displacement (BL/s)
Hour of day

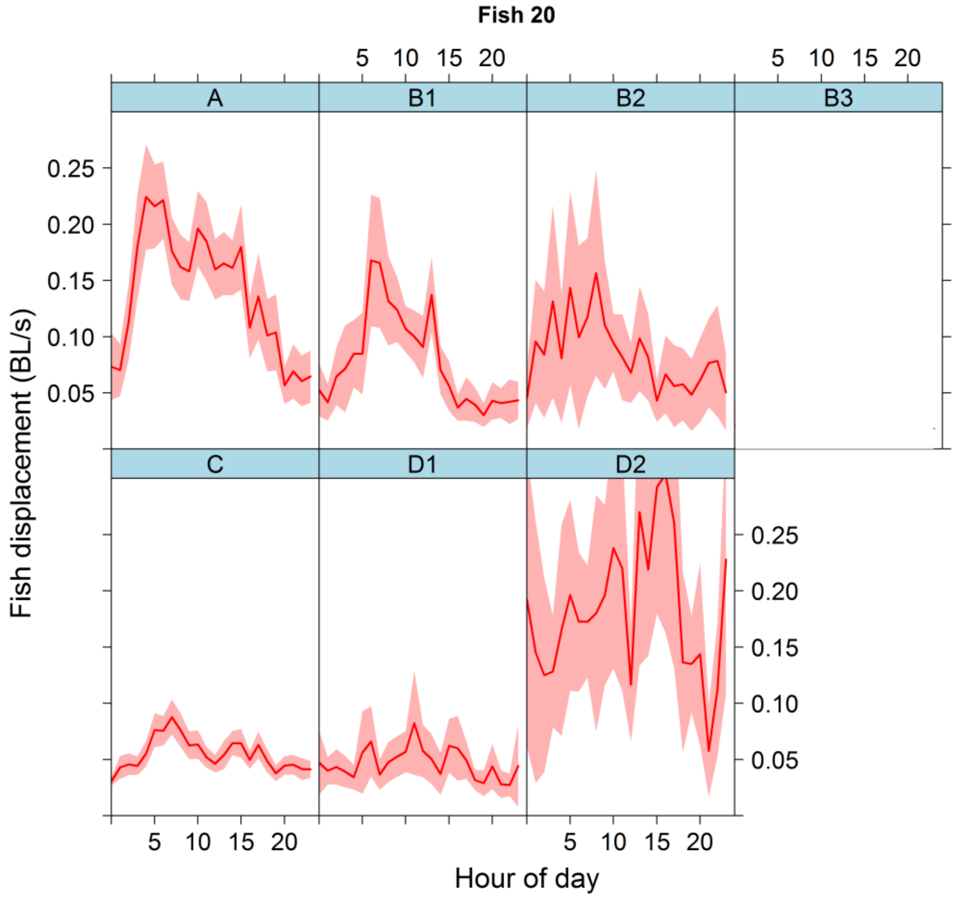
55

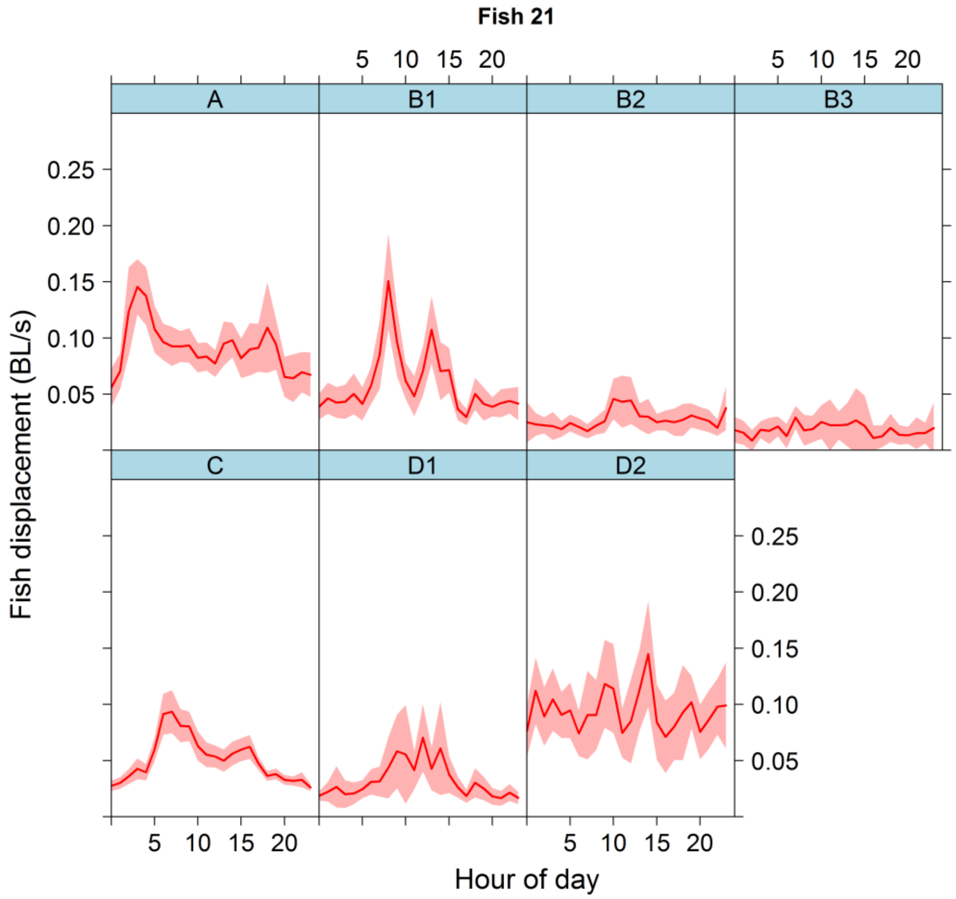

Fish 17
A
B1
B2
B3
C
0.25
0.20
0.15
0.10
0.05
5
10
15
20
Fish displacement (BL/s)
Hour of day

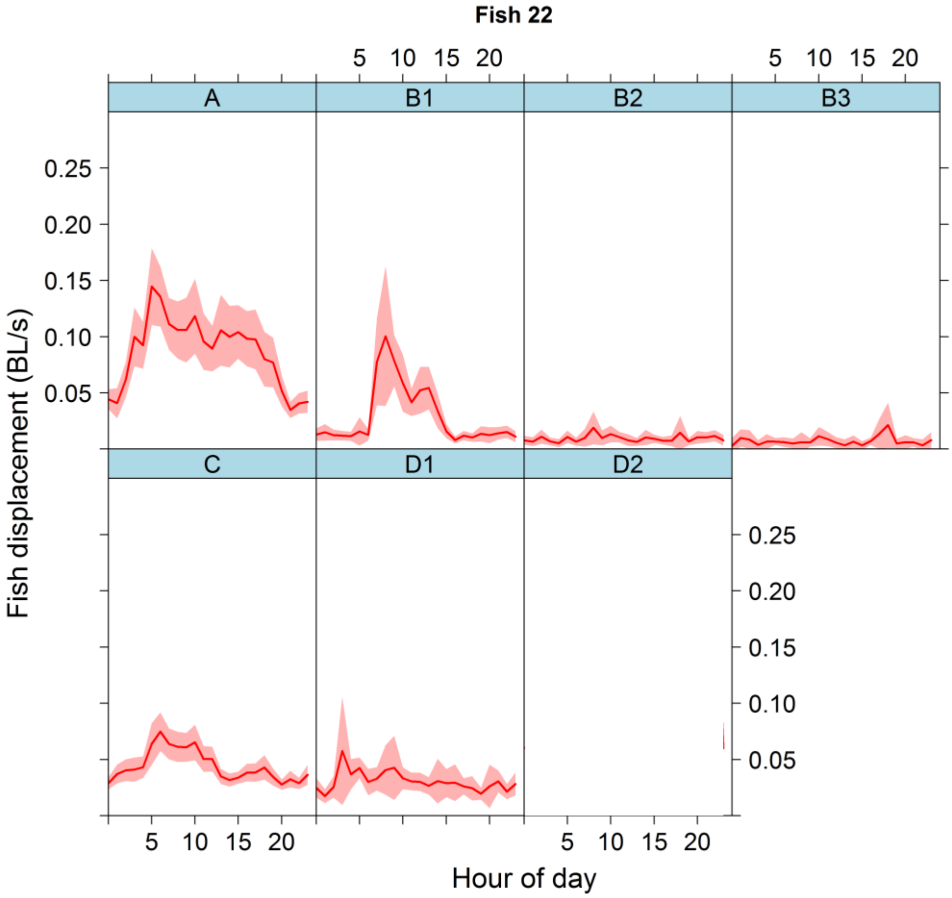
56

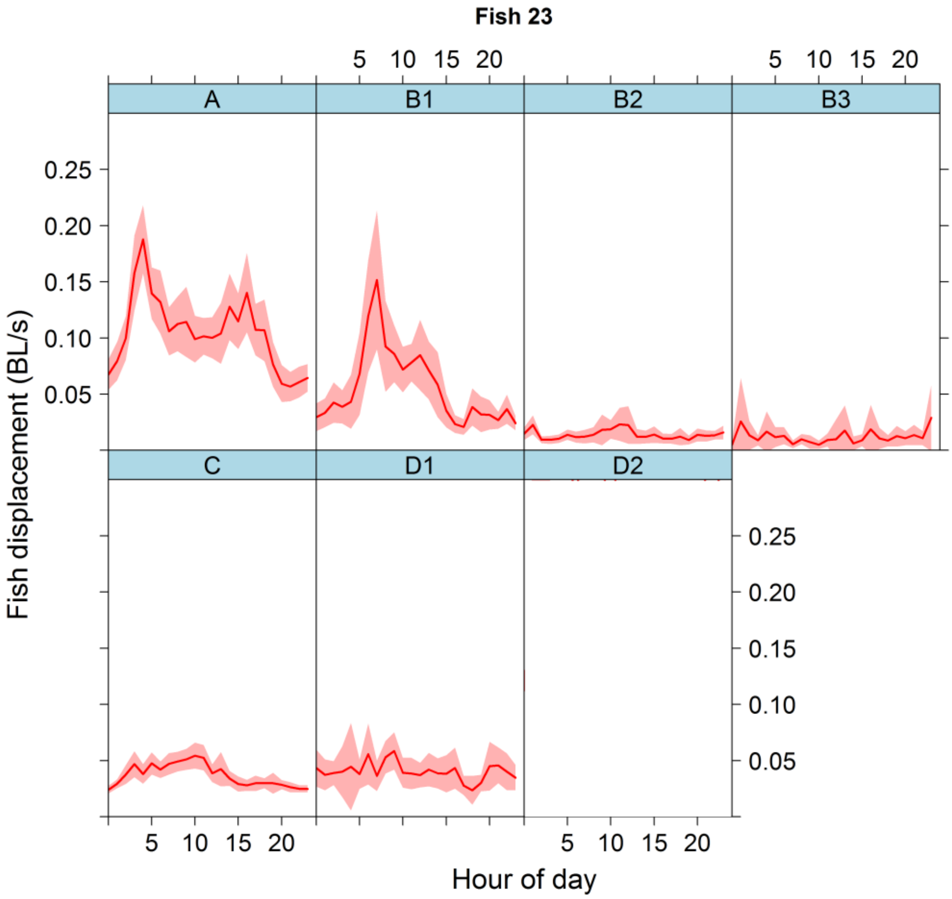

Fish 18
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.05
0.10
0.15
0.20
0.25
5 10 15 20
Hour of day


Fish 19
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.05
0.10
0.15
0.20
0.25
5 10 15 20
Hour of day


Fish 20
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.05
0.10
0.15
0.20
0.25
5
10
15
20
Hour of day

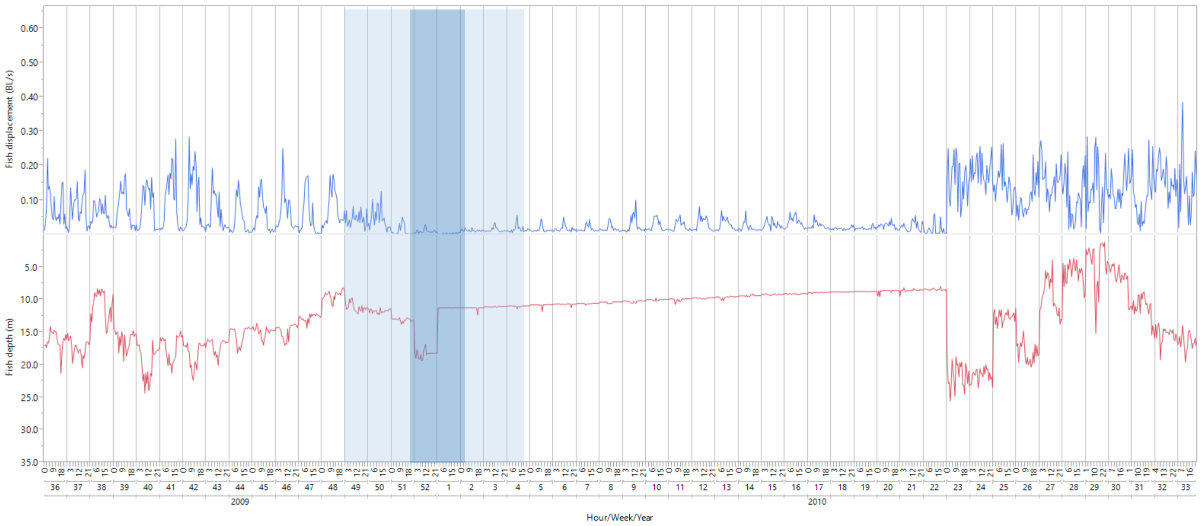

Fish 21
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.05
0.10
0.15
0.20
0.25
5
10
15
20
Hour of day


Fish 22
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.05
0.10
0.15
0.20
0.25
5
10
15
20
Hour of day

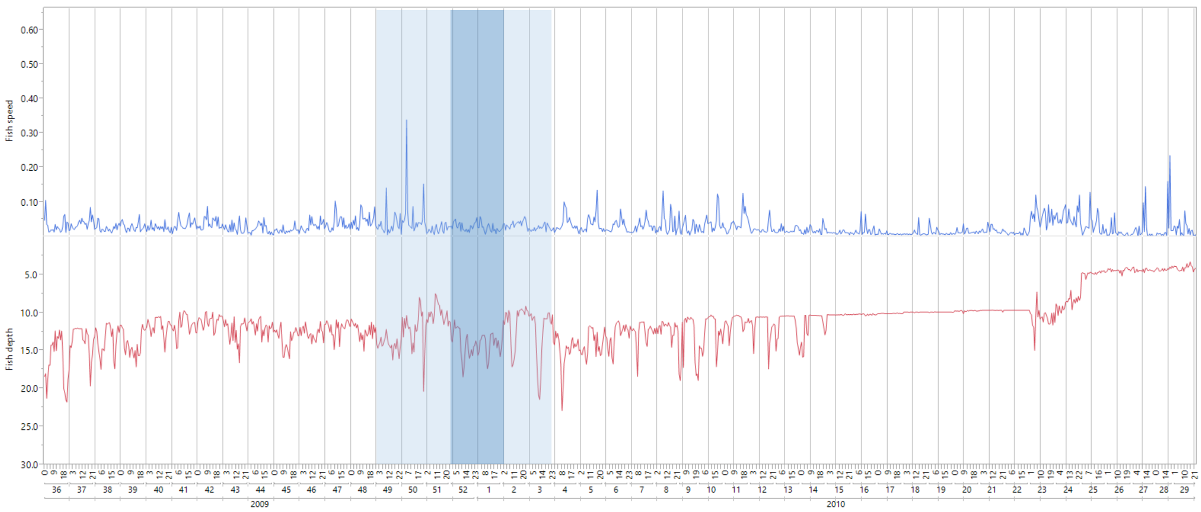

Fish 23
A
B1
B2
B3
C
D1
D2
Fish displacement (BL/s)
0.05
0.10
0.15
0.20
0.25
5
10
15
20
Hour of day

Individual figures of fish tracking data. Hourly mean values of fish displacement (body lengths per second, BLs^{-1}) and fish depth (negative m) calculated per calendar week for individual tracked Arctic charr from Lake Ellasjøen. Shading represents the period when twilight is absent (sun more than 6 degrees below the horizon, weeks 49–3) and the darkest winter solstice period (weeks 52,1). Track duration differs for individuals, *n* and ecomorph (littoral or pelagic) of individual is stated.

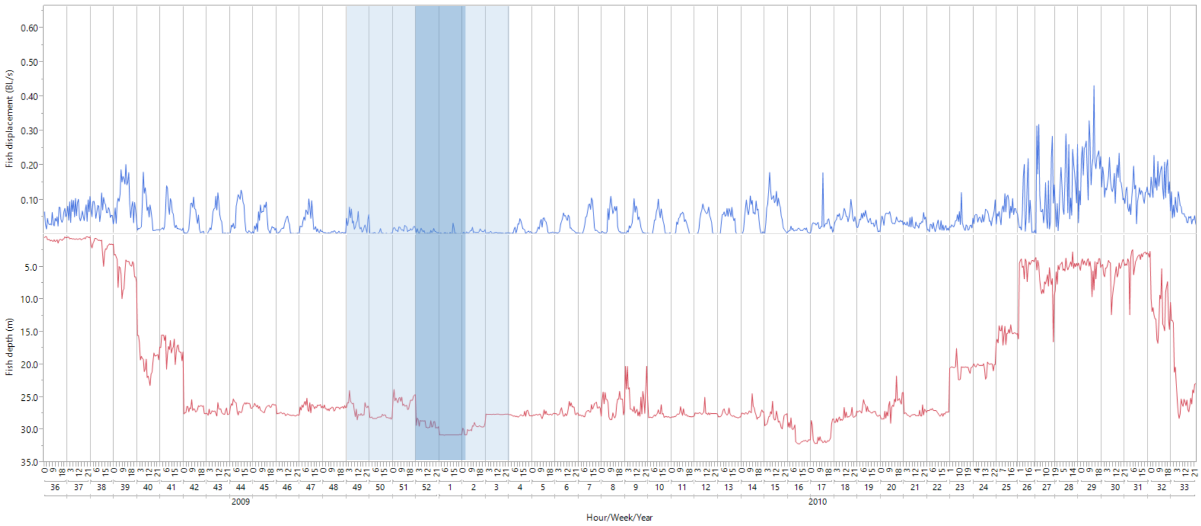
Fish 1-Littoral (n = 1,196)



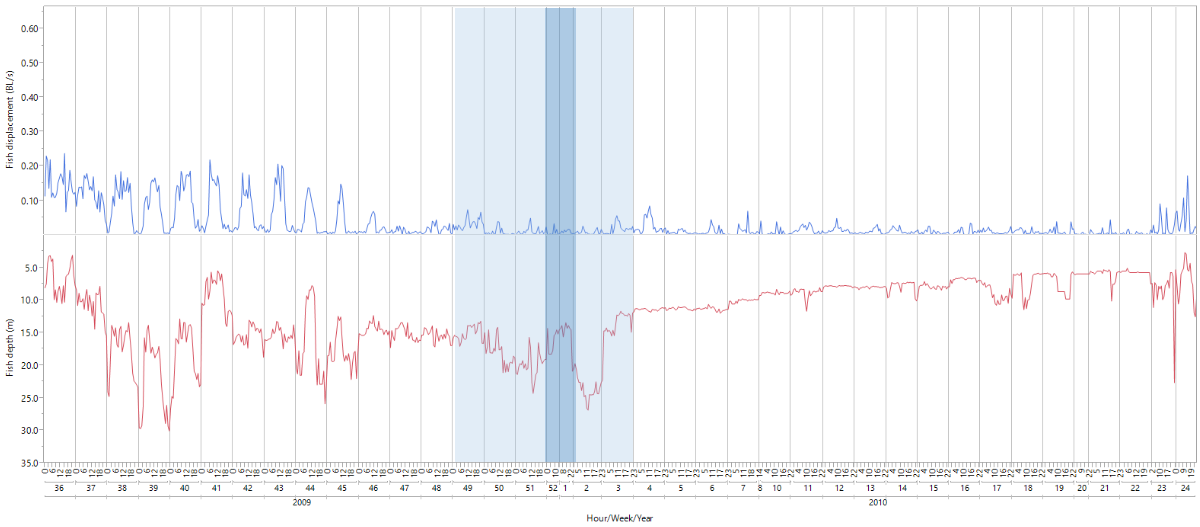
Fish 2-Littoral (n = 1,082)



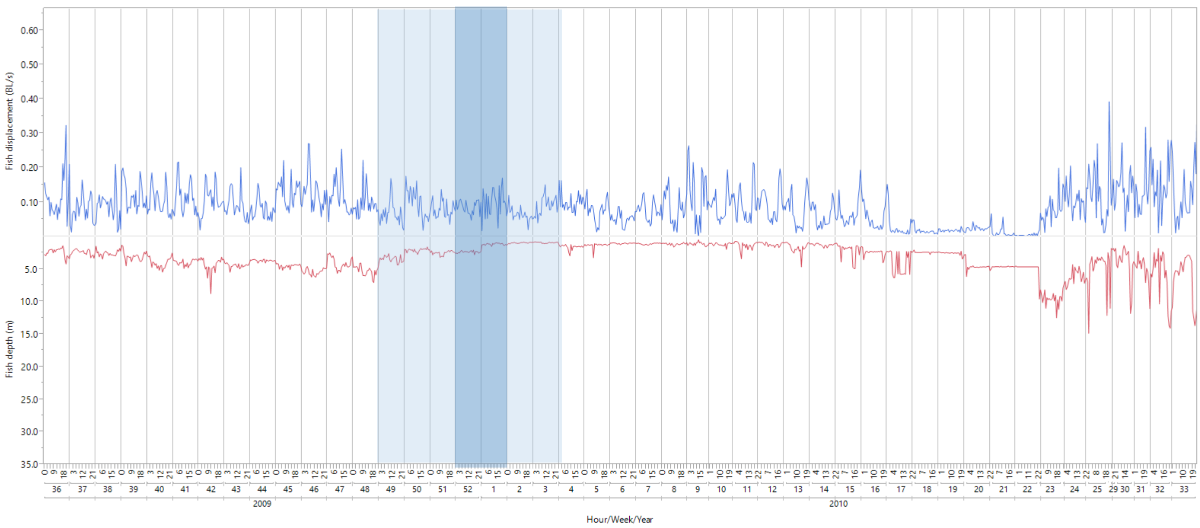
Fish 3-Littoral (n = 1,191)



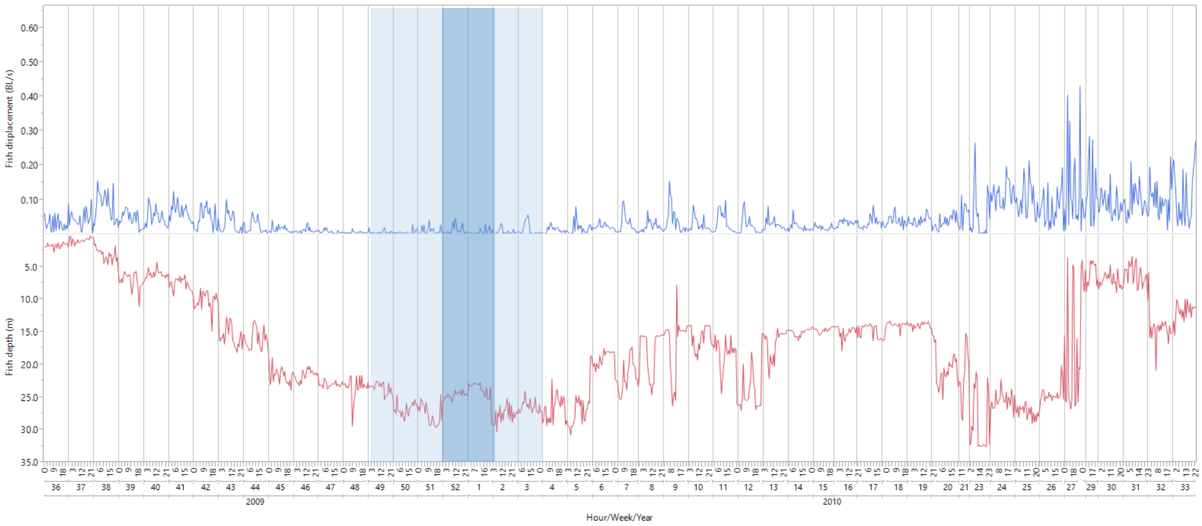
Fish 4-Littoral (n = 881)



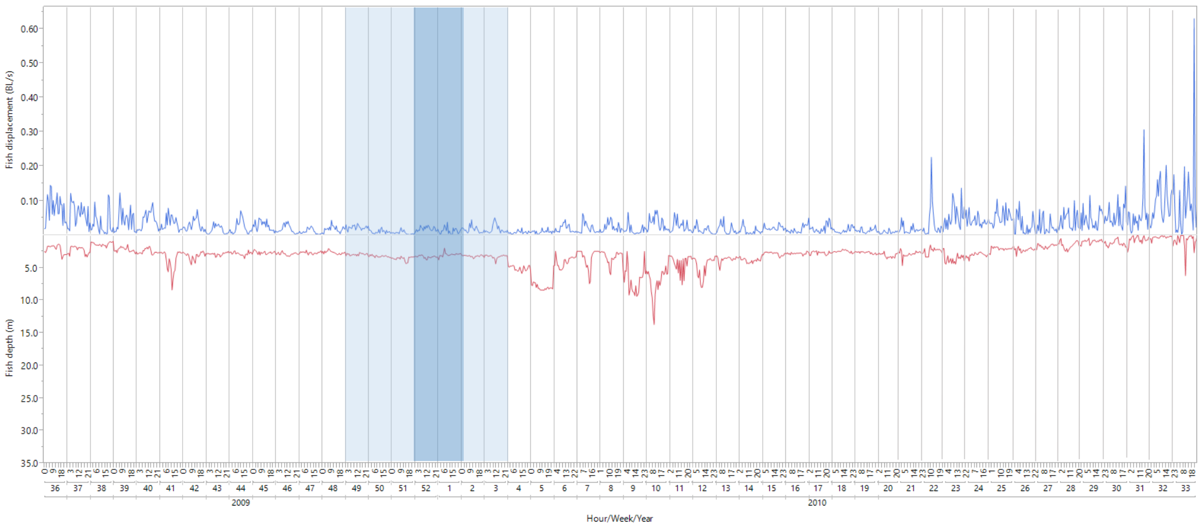
Fish 5-Littoral (n = 1,076)



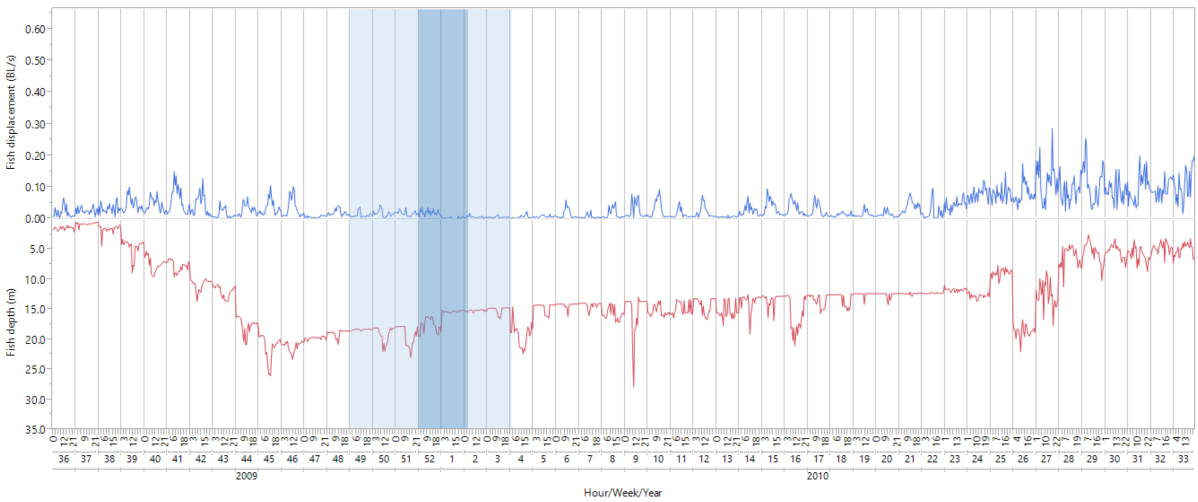
Fish 6-Littoral (n=1,104)



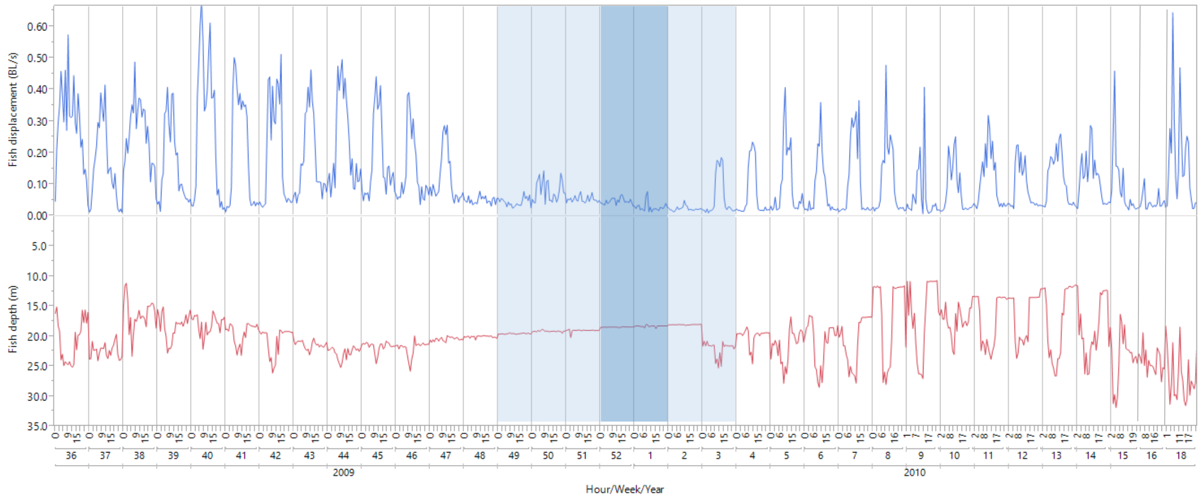
Fish 7-Littoral (n =1,187)



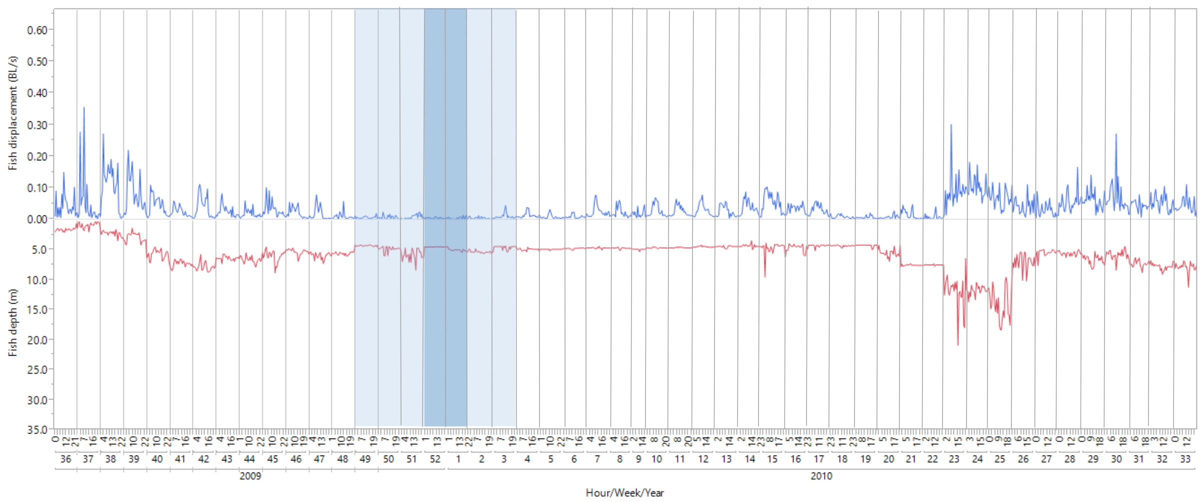
Fish 8-Littoral (n = 1,194)



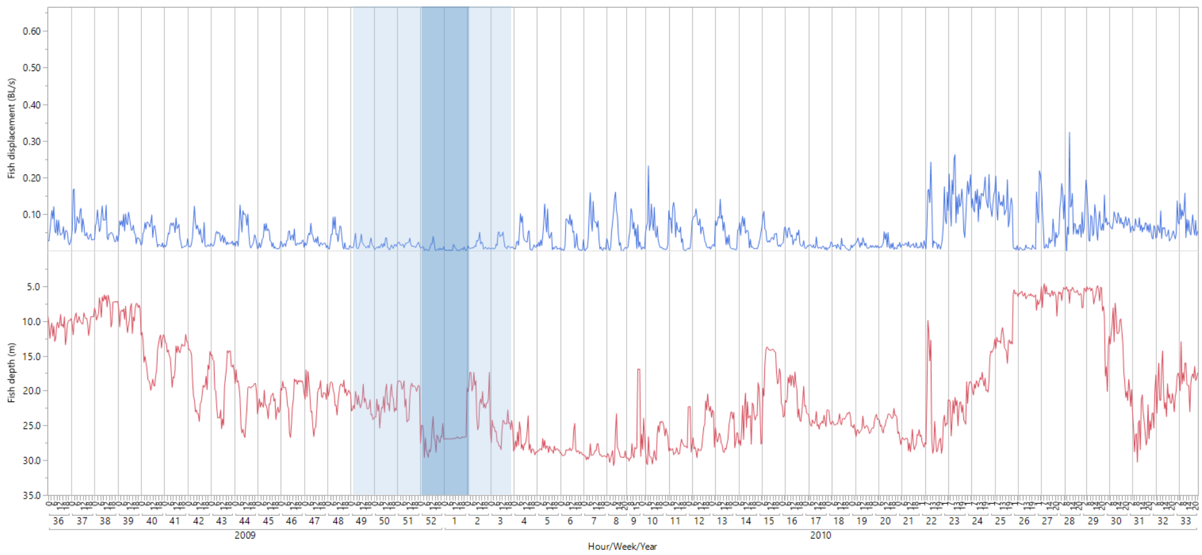
Fish 9-Littoral (n = 1,053)



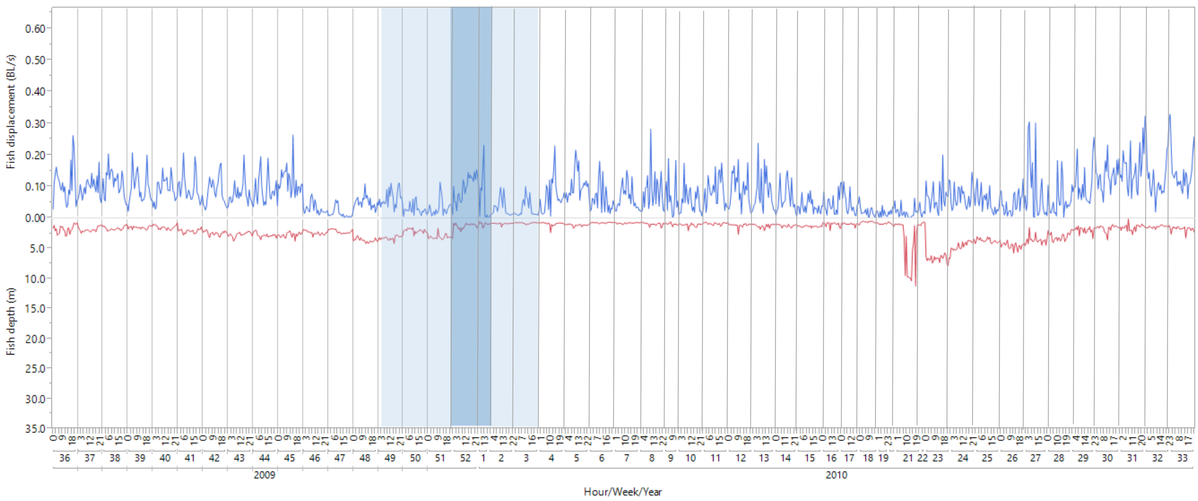
Fish 10-Littoral (n = 1,185)



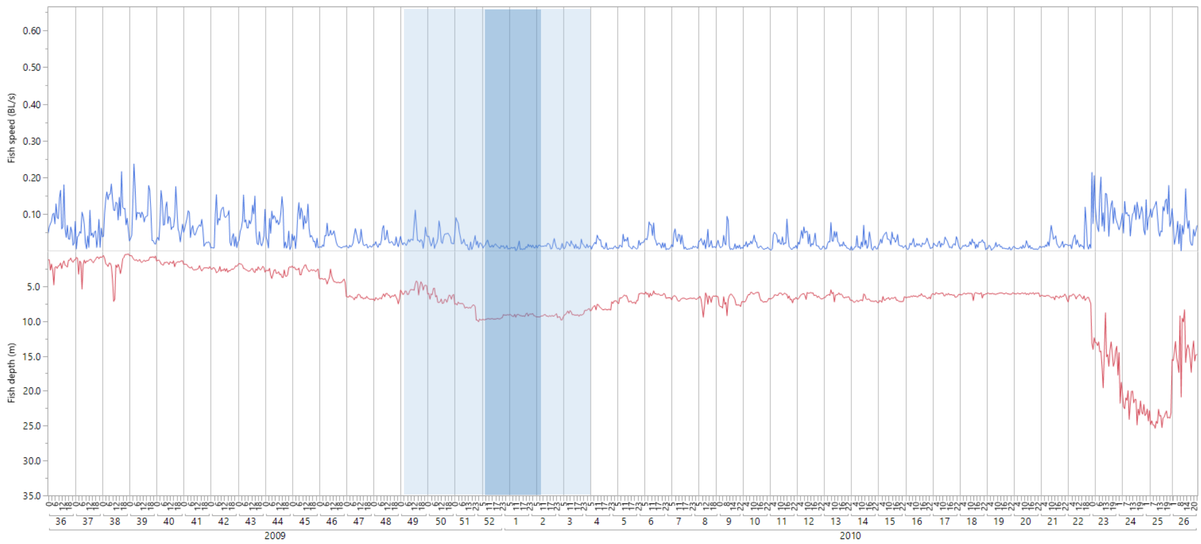
Fish 11-Littoral (n = 1,185)



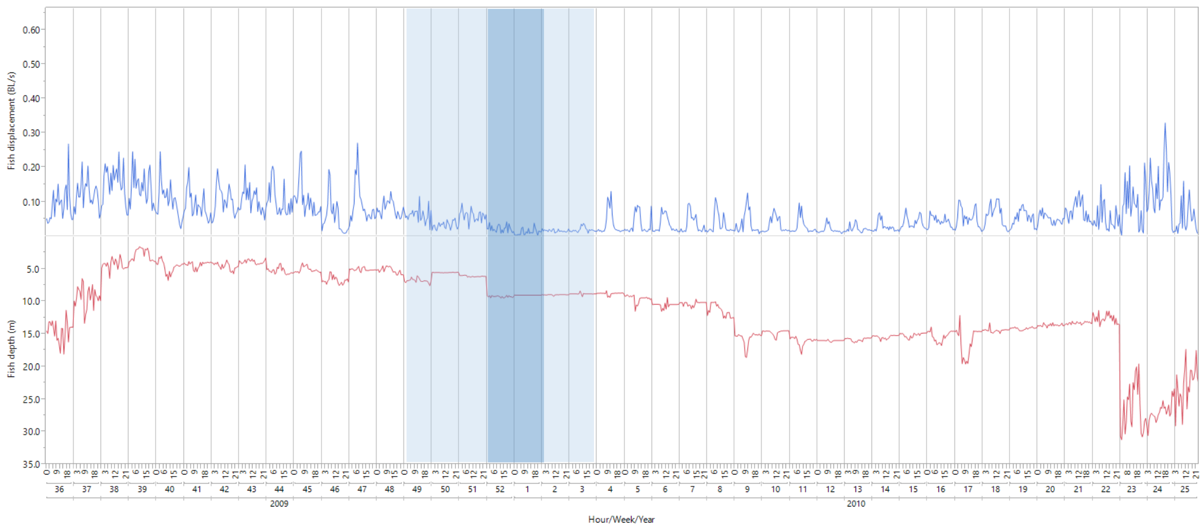
Fish 12-Littoral (n= 1,097)



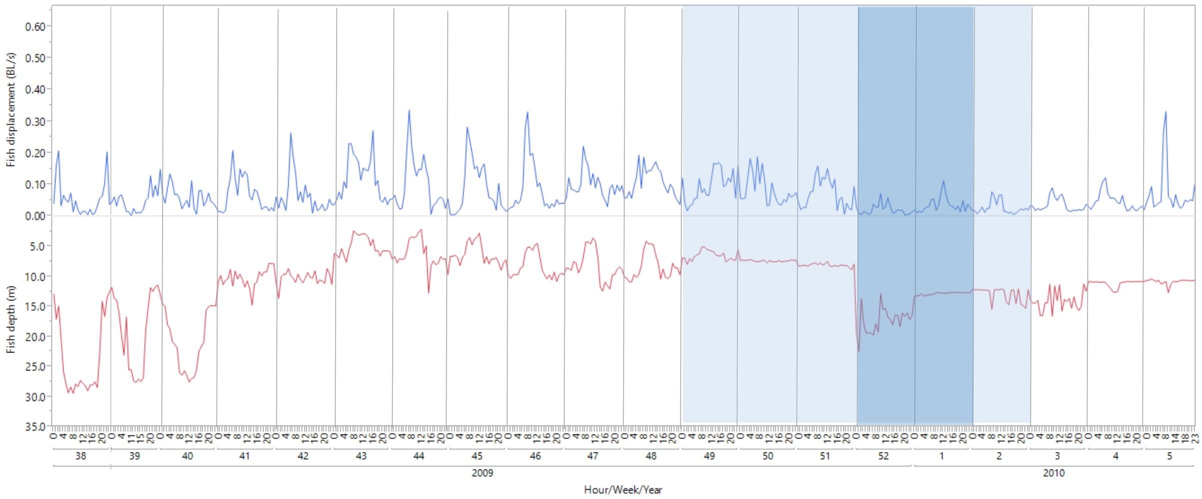
Fish 13-Littoral (n = 1,016)



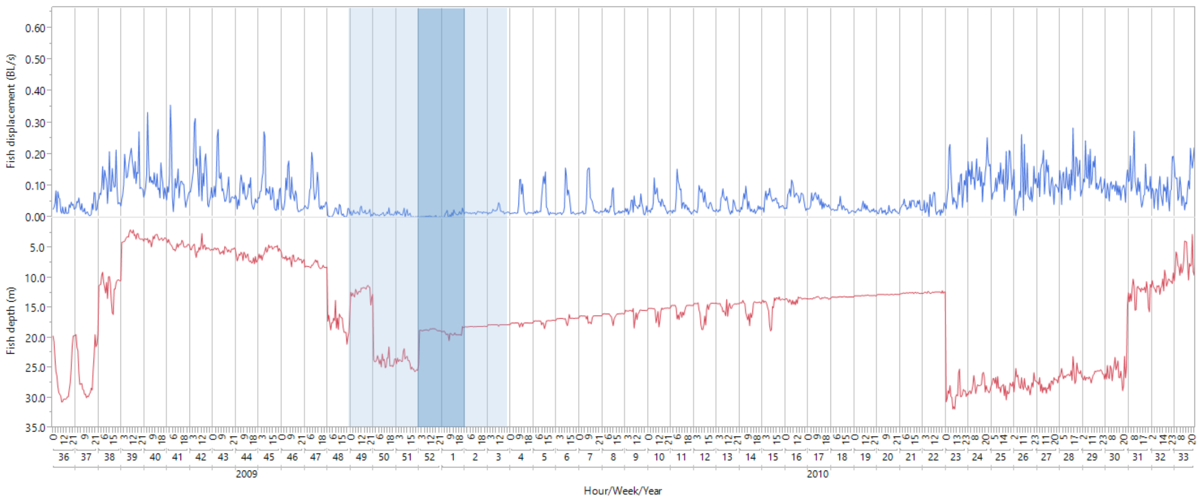
Fish 14-Pelagic (n = 1,005)



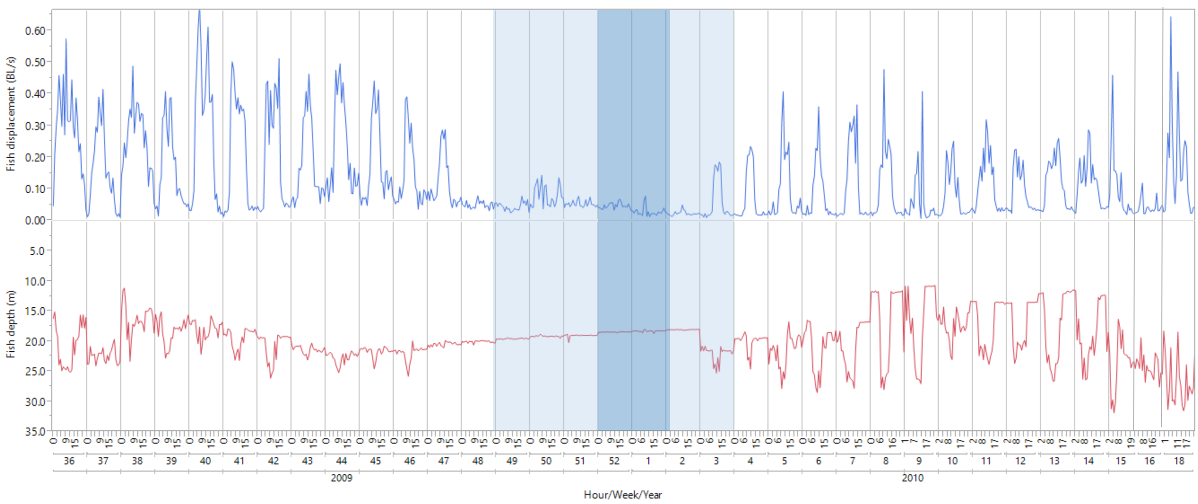
Fish 15-Pelagic (n = 472)



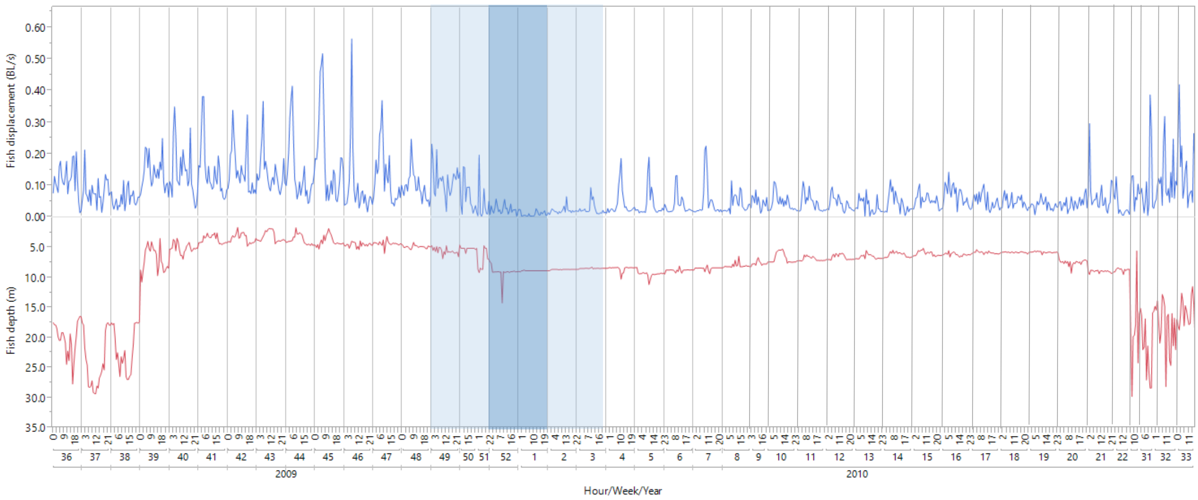
Fish 16-Pelagic (n = 942)



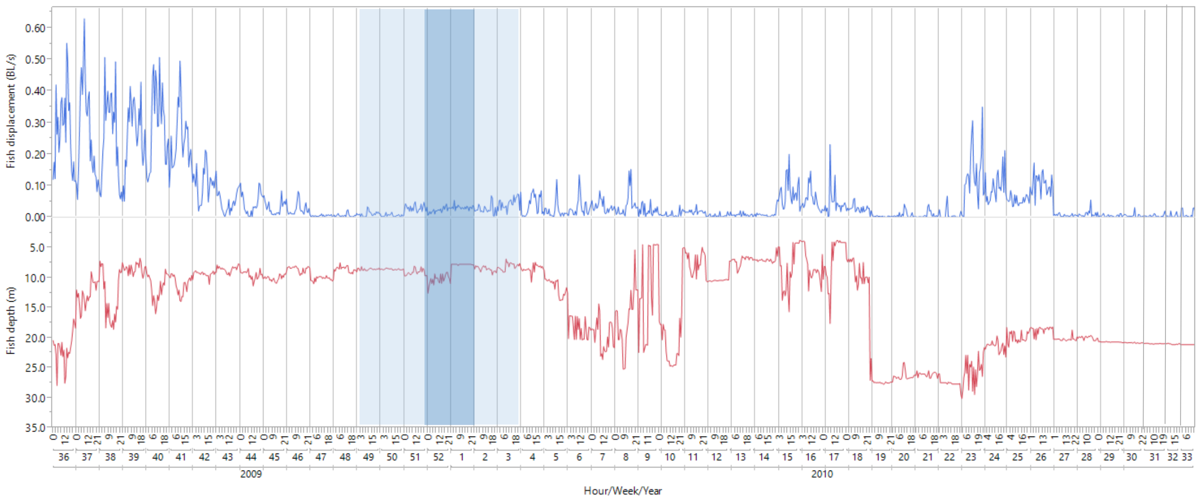
Fish 17-Pelagic (n = 813)



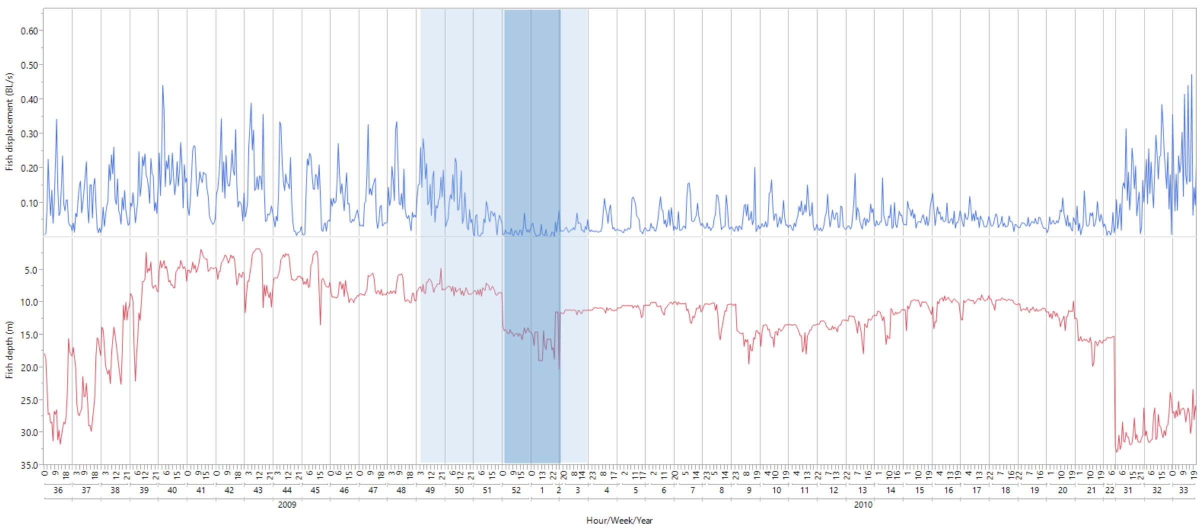
Fish 18-Pelagic (n = 942)



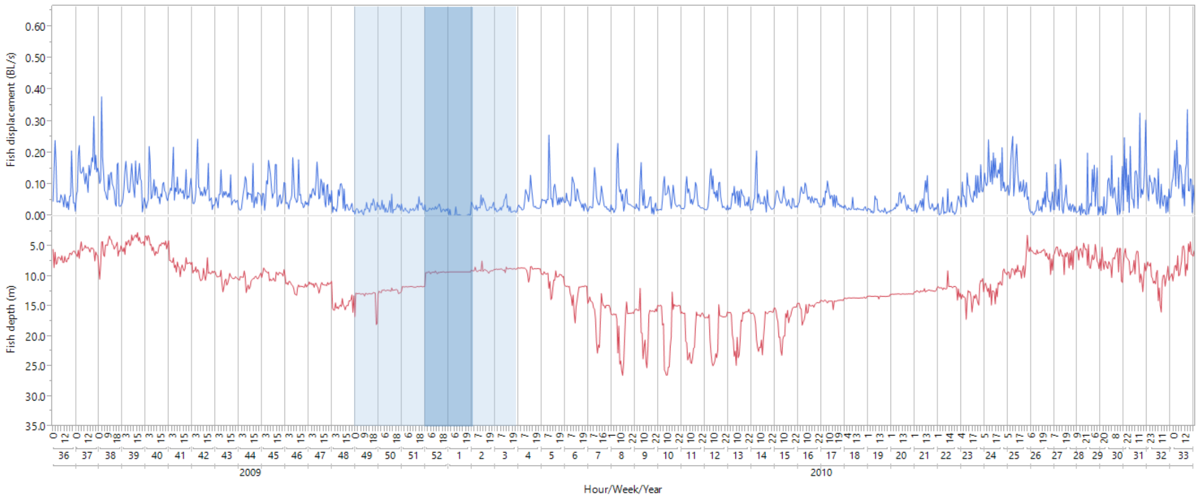
Fish 19-Pelagic (n = 1,161)



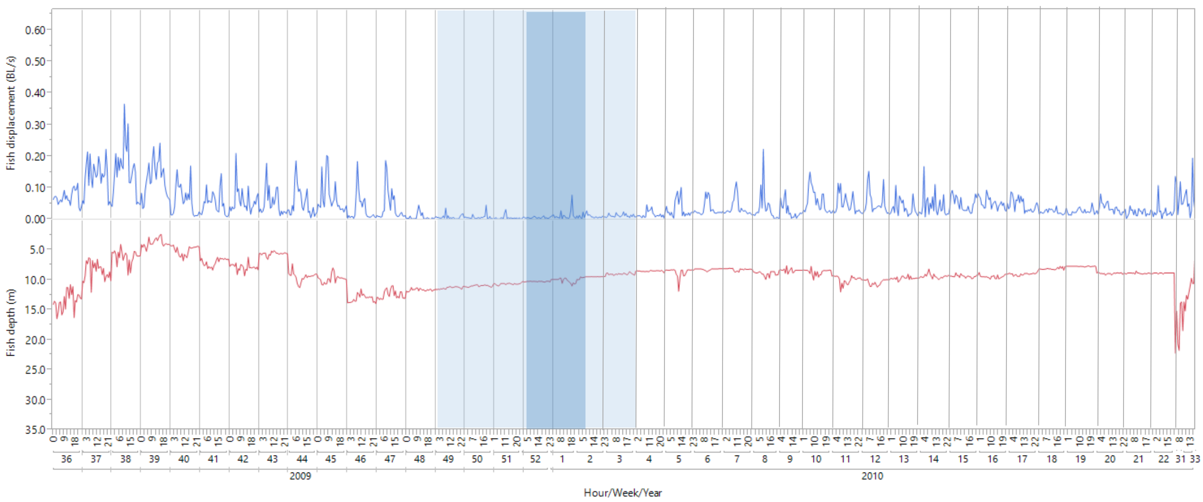
Fish 20-Pelagic (n = 952)



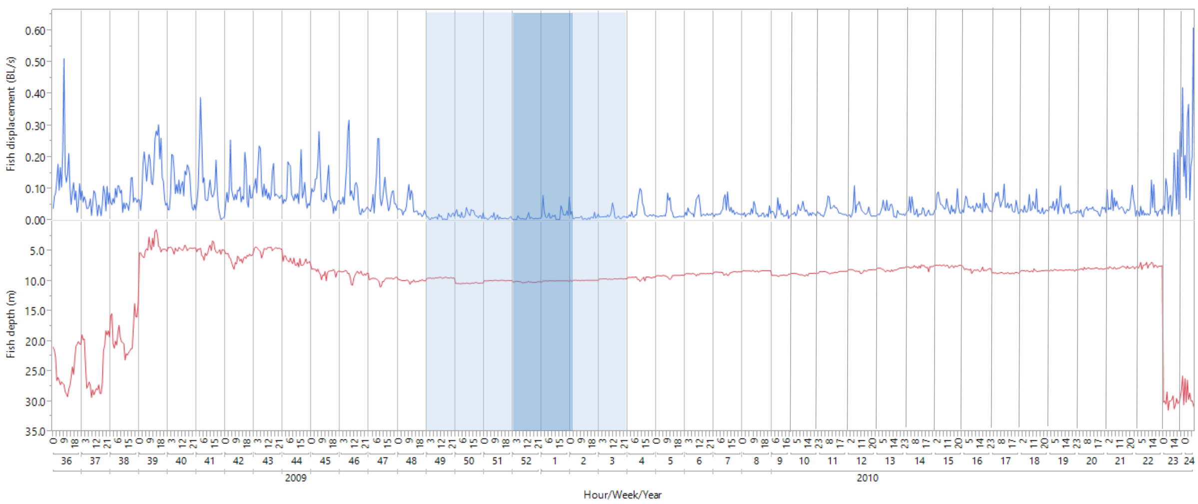
Fish 21-Pelagic (n = 1,176)



Fish 22-Pelagic (n = 928)



Fish 23-Pelagic (n = 954)



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